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THE GENUS *THURIDILLA* (OPISTHOBRANCHIA: ELYSIIDAE) FROM THE TROPICAL INDO-PACIFIC, WITH A REVISION OF THE PHYLOGENY AND SYSTEMATICS OF THE ELYSIIDAE

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ABSTRACT: This paper reviews the systematics and phylogeny of the sacoglossan genus *Thuridilla* from the Indo-Pacific tropics. The anatomy of seven previously determined species is described. Nine new species are named and described anatomically. These are: *T. carlsoni* sp. nov., *T. kathae* sp. nov., *T. flavomaculata* sp. nov., *T. hoffae* sp. nov., *T. albopustulosa* sp. nov., *T. undula* sp. nov., *T. neona* sp. nov., *T. indopacifica* sp. nov. and *T. multimarginata* sp. nov.

Phylogenetic analysis of the Elysiidae, presented here, demonstrates the monophyly of *Thuridilla* and its relationship to its sister taxon *Placobranchus*. Continued usage of the genera *Elysiella*, *Plattyclaya*, *Tridachia* and *Tridachiella* renders *Elysia* paraphyletic. For this reason the four genera are united with *Elysia* to preserve monophyly. *Bosellia* is also placed within the Elysiidae, as it possesses several synapomorphies with other members of the clade.

Anatomical data from these species, in addition to all other described members of the genus, were used to construct a phylogeny of *Thuridilla*.

Examination of biogeographical relationships of *Thuridilla* indicates that vicariance patterns of Indo-Pacific sister species have been largely masked by subsequent dispersal.

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INTRODUCTION

The genus *Thuridilla* Bergh, 1872, has recently been recognized as being distinct from *Elysia* Risso, 1818 (Jensen, 1992). The anatomy of several species was described and thirteen species were regarded as members of this genus by Jensen.

Species of *Thuridilla* are unlike most other members of the Elysiidae in that they are brightly colored and are found crawling out in the open rather than being cryptic and found in association with their specific algal food. Other derived morphological features differentiate *Thuridilla* from *Elysia*.

Of the thirteen described species now placed in *Thuridilla*, eleven are found in the Indo-Pacific tropics. Of the remaining two species, one is found in the Caribbean, East Atlantic and Mediterranean while the other is restricted to the Mediterranean. Several of the Indo-Pacific species are known only from their original description and the anatomy of only a few species has been described.

During the course of surveying the opisthobranch fauna of several Indo-Pacific localities, 16 species of *Thuridilla* were collected, including 9 undescribed species. In addition, a specimen of *Thuridilla picta* (Verrill, 1901), from the Bahamas, and two specimens of *Thuridilla hopei* (Verany, 1853), from the Strait of Gibraltar were examined. This paper further amplifies the morphology of previously named species and describes the new taxa.

Jensen (1992) described the two portions of the radular ribbon as ascending and descending. In the portion that she refers to as descending the cutting edge of the teeth is actually ascending. Owing to this ambiguity, the two portions are here referred to as dorsal and ventral. The ventral portion corresponds to Jensen's descending limb and the dorsal portion to the ascending limb. The ventral portion contains the older teeth and the dorsal portion the more newly formed ones.

A review of the known morphology of the genus permits a preliminary analysis of the phylogeny of the genus and comparison with other members of the Elysiidae.

Species Descriptions

1. Thuridilla bayeri (Marcus 1965)

Elysia bayeri Marcus, 1965: 270, figs. 5, 6; Carlson and Hoff, 1978:91, figs. 4, 5b, 6a, b.
Thuridilla bayeri (Marcus) Jensen, 1992: 273, figs. 14e, 15f, 16g–i, 17c, 18c.
Elysia ratna Marcus, 1965: 270, figs. 7, 8; Carlson and Hoff, 1978: 107, figs. 5e, 16d, e, 18.
Thuridilla ratna (Marcus) Jensen, 1992: 270, figs. 14b, 15d, 16a–c, 17a, 18b; Wells and Bryce, 1993: 64, fig. 66.

Material Examined. — Specimens with coloration more similar to *T. bayeri*: CASIZ 065743, one specimen, dissected, harbor wharf, Madang, Papua New Guinea, 10 m depth, 15 January 1988, T. M. Gosliner. CASIZ 086385, one specimen, barrier reef wnw of Rasch Passage, 4 m depth, 14 June 1992, T. M. Gosliner. CASIZ 072919, one specimen, Daphne's Reef, between Wongat and Sinub Islands, 15 m depth, 1 October, 1986, T. M. Gosliner. CASIZ 071469, one specimen, dissected, Saint Crispin Reef, nw of Port Douglas, Queensland, Australia, 15–20 m depth, 9 December 1984, M. L. Gosliner. CASIZ 087123, one specimen, under rock, Montehage Island, Manado, Sulawesi Indonesia, 3 m depth, 17 May 1990, P. Fiene-Severns. CASIZ 099057, one specimen, radula removed, pinnacle, G. Buoy, Kwajelin Atoll, Marshall Islands, 6 m depth, 5 March 1994, S. Johnson.

Specimens with coloration resembling that described for *T. ratna*: CASIZ 078470, one specimen, dissected, Sapi Island, off Kota Kinabalu, Sabah, Borneo, Malaysia, 16 m depth, 24 July 1991, T. M. Gosliner. CASIZ 072917, one specimen, jetty, Christensen Research Institute, Madang, Papua New Guinea, 13 m depth, 3 October 1986, T. M. Gosliner. CASIZ 078471, Kapas Island, off Marang, s. of Kuala Terengganu, Malaysia, 4 m depth, 28 July 1991, T. M. Gosliner. CASIZ 083866, one specimen, Twin Rocks, sw end of Calumpan Peninsula, w. of Batangas Bay, Luzon Island, Philippines, 10 m depth, 26 February 1992, T. M. Gosliner. CASIZ 086663, two specimens, Maragajong, Flores, Indonesia, under rock, 1 m depth, 27 April, 1992, P. Fiene-Severns. CASIZ 070318, one specimen, Banne de Gorgone, Nosy Bé, Madagascar, 15 April 1989, T. M. Gosliner. CASIZ 071294, one specimen, w. point of Coror Island, wreck of fishing boat, Philippines, 10–13 m depth, 5 June 1988, R. Van Syoc. CASIZ 099058, one specimen, radula removed, reef near M. M. D. C., Palau Koror, 10 m depth, M. T. Ghiselin.

Distribution. — Specimens with *T. bayeri* coloration are known from the Maldives (Yonow, 1994), the Marshall Islands (Marcus, 1965; Johnson and Boucher, 1983), Guam (Carlson and Hoff, 1978; Jensen, 1992), ? Fiji (Brodie and Brodie, 1990), Papua New Guinea (present study), Indonesia (present study), Australia (present study). Specimens with coloration resembling *T. ratna* are known from Palau (Marcus, 1965; present study), Guam and Ponape (Carlson and Hoff, 1978), Marshall Islands (Johnson and Boucher, 1983; Scott Johnson, pers. comm.), eastern and Western Australia (Jensen, 1992; present study), Thailand (Jensen, 1992), Philippines (present study), Indonesia (present study), Malaysia (present study), Madagascar (present study).

External Morphology. — The living animals (Fig. 1A, B) are 12–20 mm in length. Specimens with coloration typical of *T. bayeri* are dark brown to black with a series of 6–10 cream to yellow longitudinal lines on the head and parapodia. The edge of the parapodia may be lined with an orange to red-orange line (a single specimen from Papua New Guinea), an absence of other pigment giving the impression of a row of black spots (specimens from Guam)

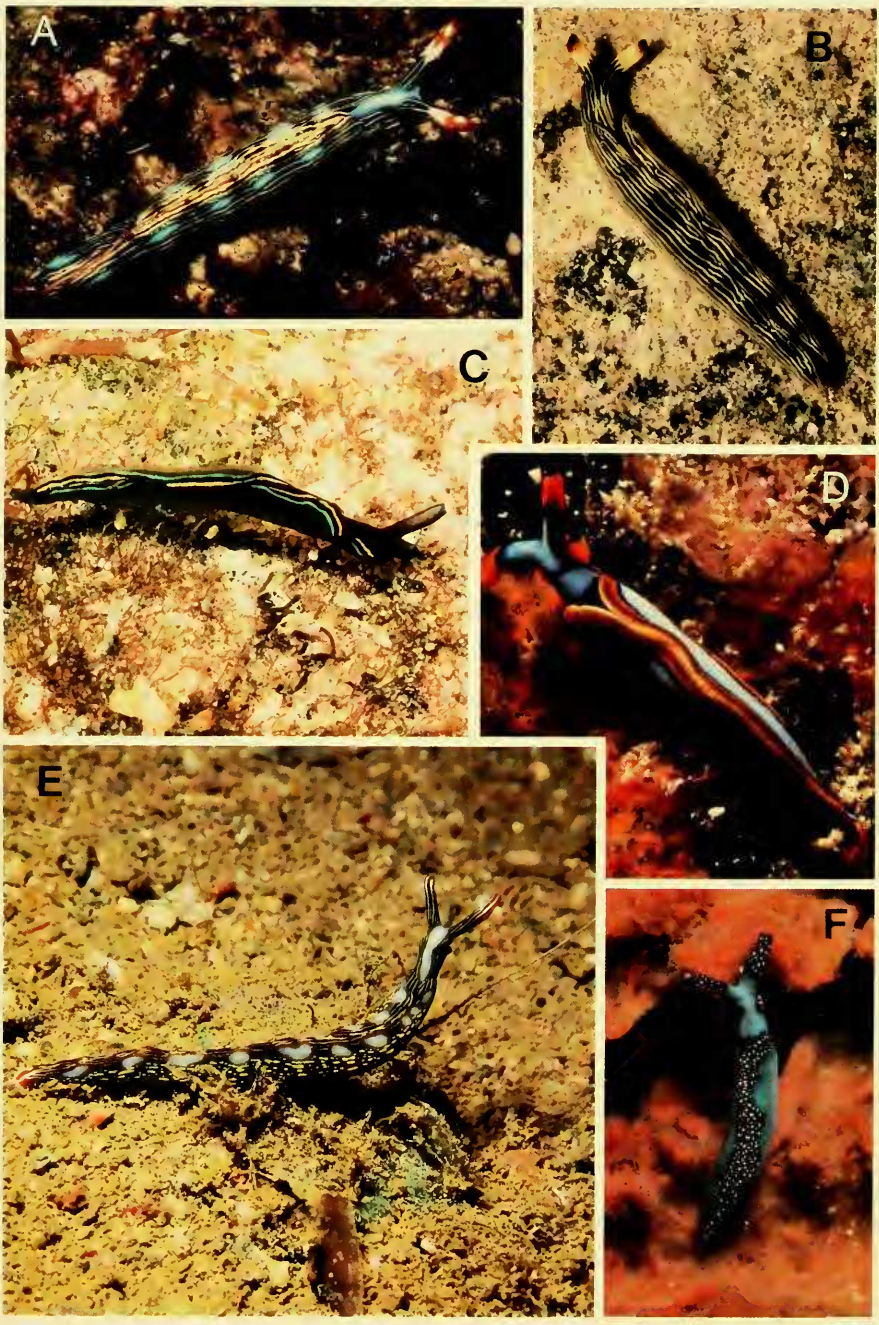

FIGURE 1. Living animals. A. *Thuridilla bayeri* (Marcus, 1965), Madang, Papua New Guinea, 20 mm in length. B. *Thuridilla bayeri* (Marcus, 1965), with coloration typical of *T. ratna* Marcus, 1965, Nosy Bé, Madagascar, 15 mm in length. C. *Thuridilla livida* (Baba, 1955), Sodwana Bay, South Africa, 17 mm in length. D. *Thuridilla lineolata* (Bergh, 1905), Manado, Indonesia, photograph by Pauline Fiene-Severns, 20 mm in length. E. *Thuridilla splendens* (Baba, 1949), Okinawa, photo by Robert F. Bolland, 25 mm in length. F. *Thuridilla moebii* (Bergh, 1888), Sodwana Bay, South Africa, 12 mm in length.

or bluish green patches (specimens from the Marshall Islands). Other specimens lack any additional pigment along the margin of the parapodia. Red-orange pigment may be present at the posterior junction of the parapodia. Six to seven bright blue, ovoid spots are found submarginally along the length of each parapodium. The head may also have a mid-dorsal blue mark or paired spots between the rhinophores. Basally, the rhinophores are the same color as the general body, with cream longitudinal lines. These lines expand and unite into a large transverse white band. This band may continue to the apex of the rhinophores or may be followed by a red band or streaks. A single specimen from the Solomon Islands (Scott Johnson, pers. comm.) has an additional apical black ring distal to the red ring. In specimens from the Marshall Islands, there is considerable variation in the presence of the white and red pigment on the rhinophores. Only white pigment may be present or there may be longitudinal red streaks that merge with the white band. The anterior margin of the foot is red, often with opaque white. Blue spots may also be present on the anterior portion of the foot. In specimens with heavy blue spotting, the inside of the parapodia has a narrow white marginal band, a broad orange band, and a broader black area. Inside the black band is an area of bright blue pigment. The coloration of the inside of the parapodia is not known from specimens with little blue pigment.

In specimens with coloration typical of *T. ratna*, the animal is dark brown with eight to ten white or cream lines along the outer side of the parapodia and on the head. The internal margin of the parapodia is usually orange. The posterior junction of the parapodia may contain some orange pigment. The head is the same color as the parapodia, without any additional pigment. Basally, the rhinophores are the same color as the remainder of the body. In some specimens, the white or cream lines widen distally and form a transverse band. In most specimens, some red or red-orange pigment may be present on the rhinophores. This may be present as a series of red longitudinal lines or a distinct transverse band. An apical transverse black band may also be present on the rhinophores. Its presence is independent of the presence of red pigment. The margin of the anterior end of the foot is red or orange. The inside of the parapodia is usually brownish with scattered turquoise blue pigment. A thin, white marginal band is present and a broader, orange submarginal band may be prominent or absent.

PERICARDIUM AND DORSAL VESSELS. — In specimens with coloration typical of *T. bayeri*, the pericardium is ovoid (Fig. 2A–C). From its sides, are two lateral vessels which bifurcate terminally or remain undivided. From the posterior end of the pericardium are two other blood vessels, that are joined basally. They are bifurcate or slightly more highly branched.

The branching of the dorsal vessels was examined in four specimens with coloration typical of *T. ratna* (Fig. 2D–G). In all cases, there are both lateral and posterior vessels. In one individual, only the left lateral branch was present, but a secondary right branch was situated off the side of the right posterior branch. The lateral branches are undivided or contain bifurcate or more highly branched tips. The posterior vessels have a common origin from the pericardium. They may entirely lack branches or have a few secondary branches.

BUCCAL MASS AND RADULA. — The buccal mass (Fig. 3A) contains a round pharyngeal pouch and relatively larger, more muscular pharyngeal portion. There is no morphological difference between specimens of different color patterns. In two specimens with coloration typical of *T. bayeri*, the radula contains 24–26 teeth. There are 7–8 teeth in the dorsal portion of the radula, 7–8 in the ventral portion and 9 arranged in a spirally coiled fashion. No loose teeth were contained in the ascus. Each tooth (Fig. 4) is elongate and arched. There are 17–18 coarse denticles on either side of the tooth. The denticles continue as faint striae on the dorsal surface of the teeth.

The radula of two specimens with coloration typical of *T. ratna* consisted of 26–27 teeth (8–9 in the ventral limb, 8–9 in the dorsal limb and 9 to more than 10 loose teeth in the ascus). The teeth (Fig. 5) are triangular with the serrated portion longer than the basal one. The cutting margin bears 16–18 coarse denticles per side of the tooth.

REPRODUCTIVE SYSTEM (Fig. 3B–D). — The reproductive morphology is complex and appears complicated, due to the diffuse distribution of the ovotestis, prostatic cells and al-

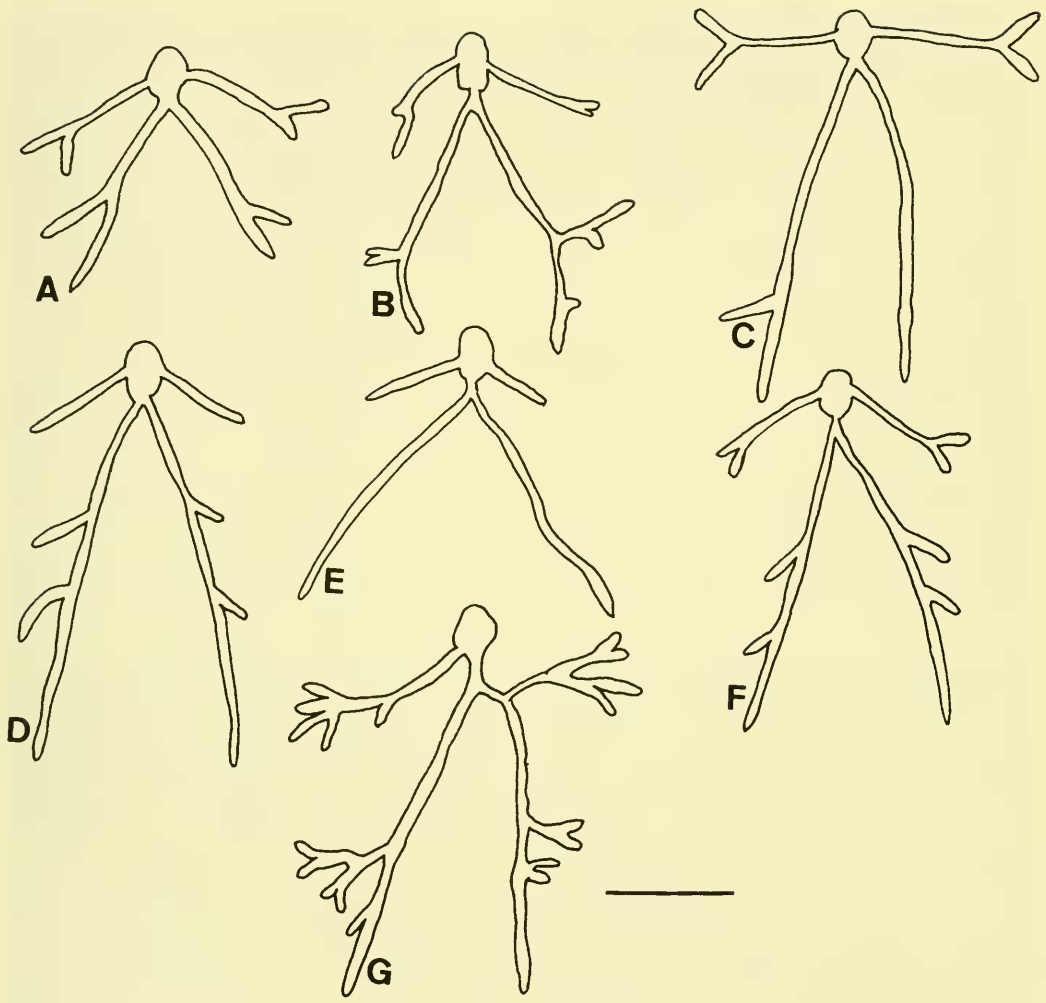

FIGURE 2. *Thuridilla bayeri* (Marcus, 1965). A–C. Variation in branching of pericardial vessels in specimens with coloration typical of *T. bayeri*. D–G. Variation in branching of pericardial vessels is specimens with coloration of *T. ratna*, *scale* = 4.0 mm.

bumen gland throughout the parapodia. The system is basically triaulic. The ovotestis contains lobate acini. They connect via a pair of elongate hermaphroditic ducts. These ducts join immediately anterior to the round, short stalked ampulla. The prostate consists of approximately six elongate finger-shaped glands. The albumen gland consists of numerous digitiform ducts with lateral glandular bodies. The prostate and albumen glands join together into a pair of ducts that join the female gland mass immediately anterior to the junction of the hermaphroditic ducts. The female gland mass consists of several distinct lobes, the largest forms the bulk of the mucous gland. Near the posterior end of the mass a spherical receptaculum seminis joins the gland mass via a thin, moderately long duct. Near the anterior end of the gland

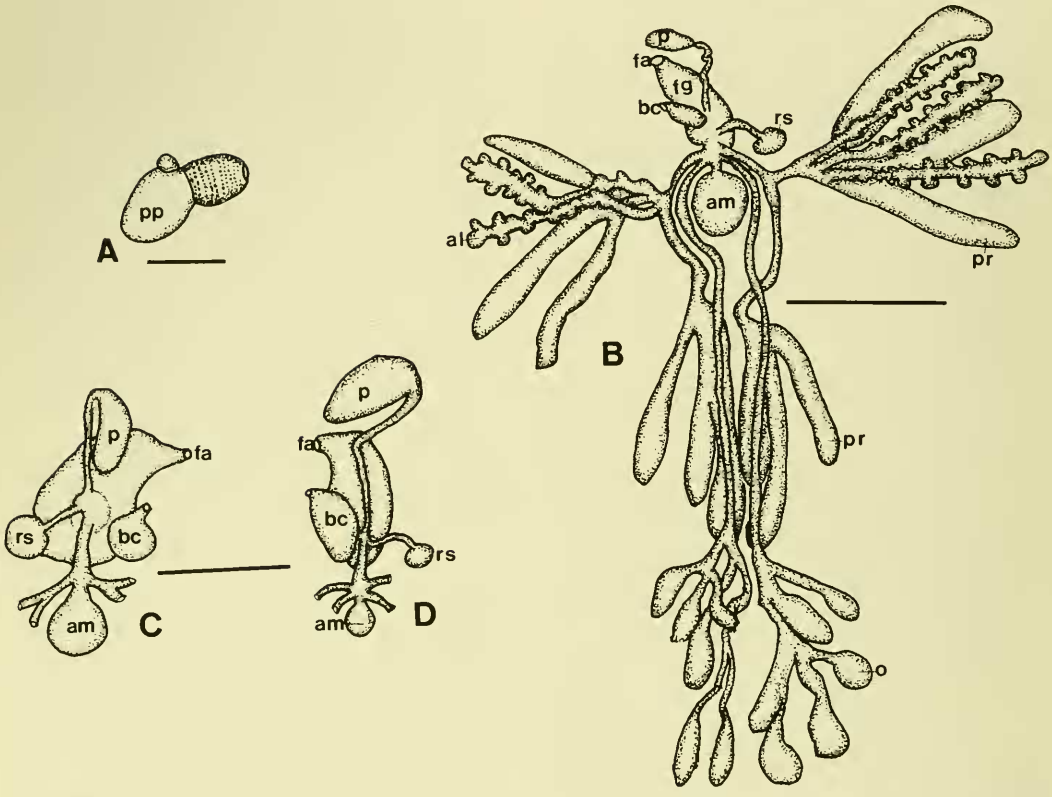

FIGURE 3. *Thuridilla bayeri* (Marcus, 1965). A. Buccal mass, pp = pharyngeal pouch, scale = 0.25 mm. B. Entire reproductive system: al = albumen gland, am = ampulla, bc = bursa copulatrix, fa =female aperture, fg = female gland mass, o = ovotestis, p = penis, pr = prostate glands, rs = receptaculum seminis, scale = 1.0 mm. C. Distal reproductive organs of specimen with color typical of *T. bayeri*, Australia. D. Distal reproductive organs of specimen with color typical of *T. ratna*. C., D., lettering same as in B., scale = 1.0 mm.

mass, the thin vas deferens emerges and joins the simple unarmed penis. A saccate bursa copulatrix emerges to the outside of the body wall near the female gonopore. The female gonopore exits into the lateral ciliated groove, adjacent to the anus. The penis exits below the right rhinophore. The reproductive morphology was examined in three specimens with coloration typical of *T. bayeri* and two with coloration characteristic of *T. ratna*.

DISCUSSION. — *Thuridilla bayeri* is similar in appearance and appears closely related to two other species, *T. ratna* and *T. splendens*. All three species are similar in having a uniformly dark blackish body with numerous longitudinal yellow or white lines. In *T. bayeri* and *T. splendens*, there are bluish markings and spots on the head and parapodia. In the latter species, there are yellow spots on the surface of the parapodia that are absent in *T. bayeri*.

Based on the similarity of color pattern, Brodie and Brodie (1990) considered *T. bayeri* and *T. ratna* as synonymous. Others (Marcus, 1965; Carlson and Hoff, 1978; Jensen, 1992) have considered them to be distinct species. Carlson and Hoff, and Jensen emphasized the distinctness of the color pattern of *T. bayeri*, blue spots along the parapodia and black spots along the parapodial margin. Carlson and Hoff (1978) also noted differences in the coloration of the inner surface of the parapodia in specimens from Guam. In *T. bayeri*, the margin of the inner portion of the parapodia is white, followed by a red-orange band, an area of black, followed by a large area of steel blue. In *T. ratna*, the submarginal red-orange band is usually absent and the inside of the parapodia is brownish, with scattered white and blue mark-

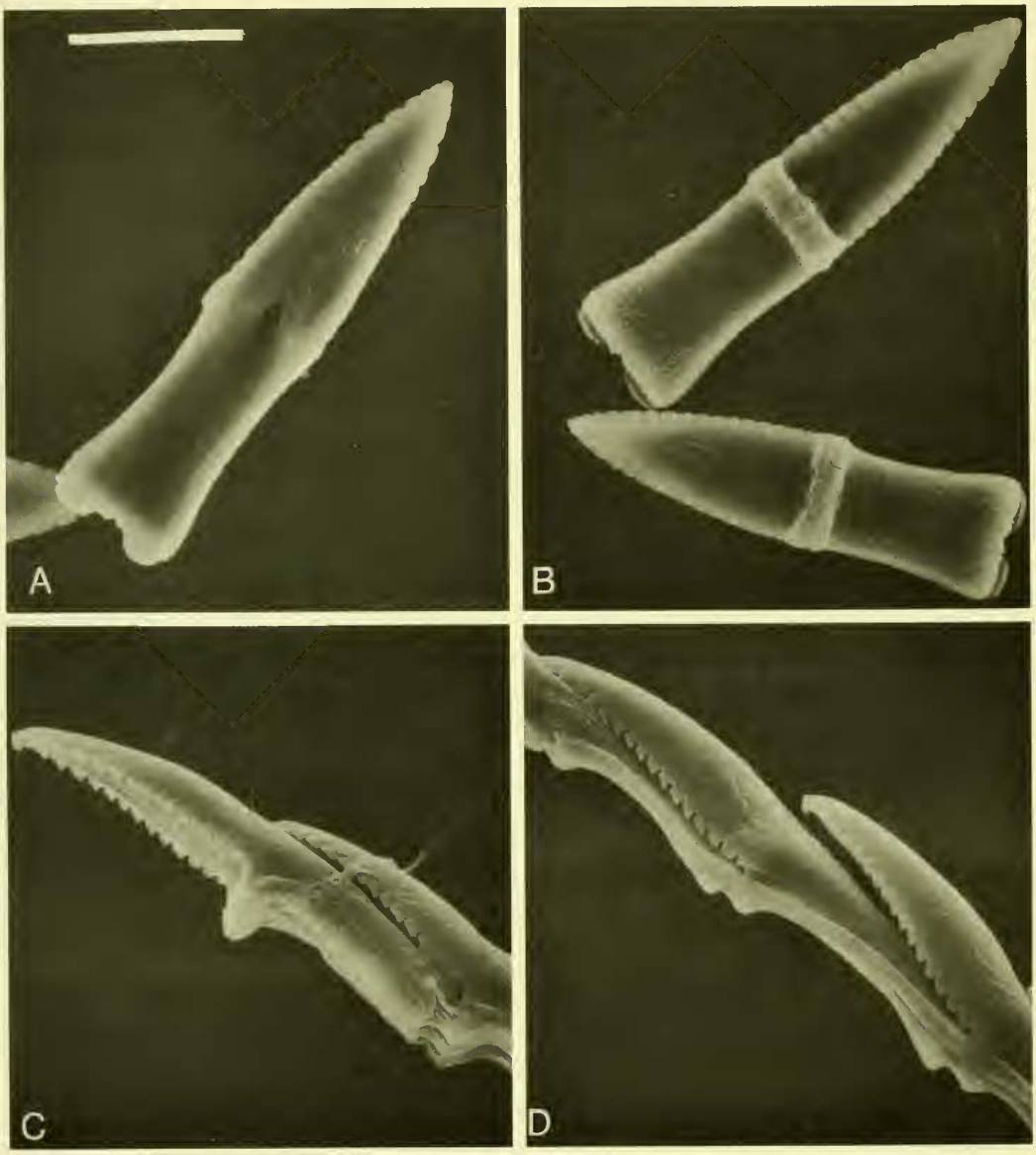

FIGURE 4. Radular teeth of specimen with color typical of *T. bayeri*. A. Dorsal view of tooth from specimen from Kwajelin, CASIZ 099057, scale = 15 μm. B. Ventral view of teeth from same radula, scale = 15 μm. C. Lateral view of tooth from specimen from Australia, CASIZ 071469, scale = 15 μm. D. Lateral view of teeth from specimen from Papua New Guinea, CASIZ 065743, scale = 15 μm.

ings. Two specimens with external coloration matching that of *T. ratna*, from Guam and Malaysia, have a prominent red submarginal band and some bluish pigment in the pericardial region. This pigment appears to be somewhat intermediate between the two species. Several specimens examined in this study further blur the distinctness of *T. bayeri*. Most specimens of *T. bayeri* have blue pigment on the dorsal surface of the head between the rhinophores and additional blue on the anterior portion of the foot. One specimen from Papua New

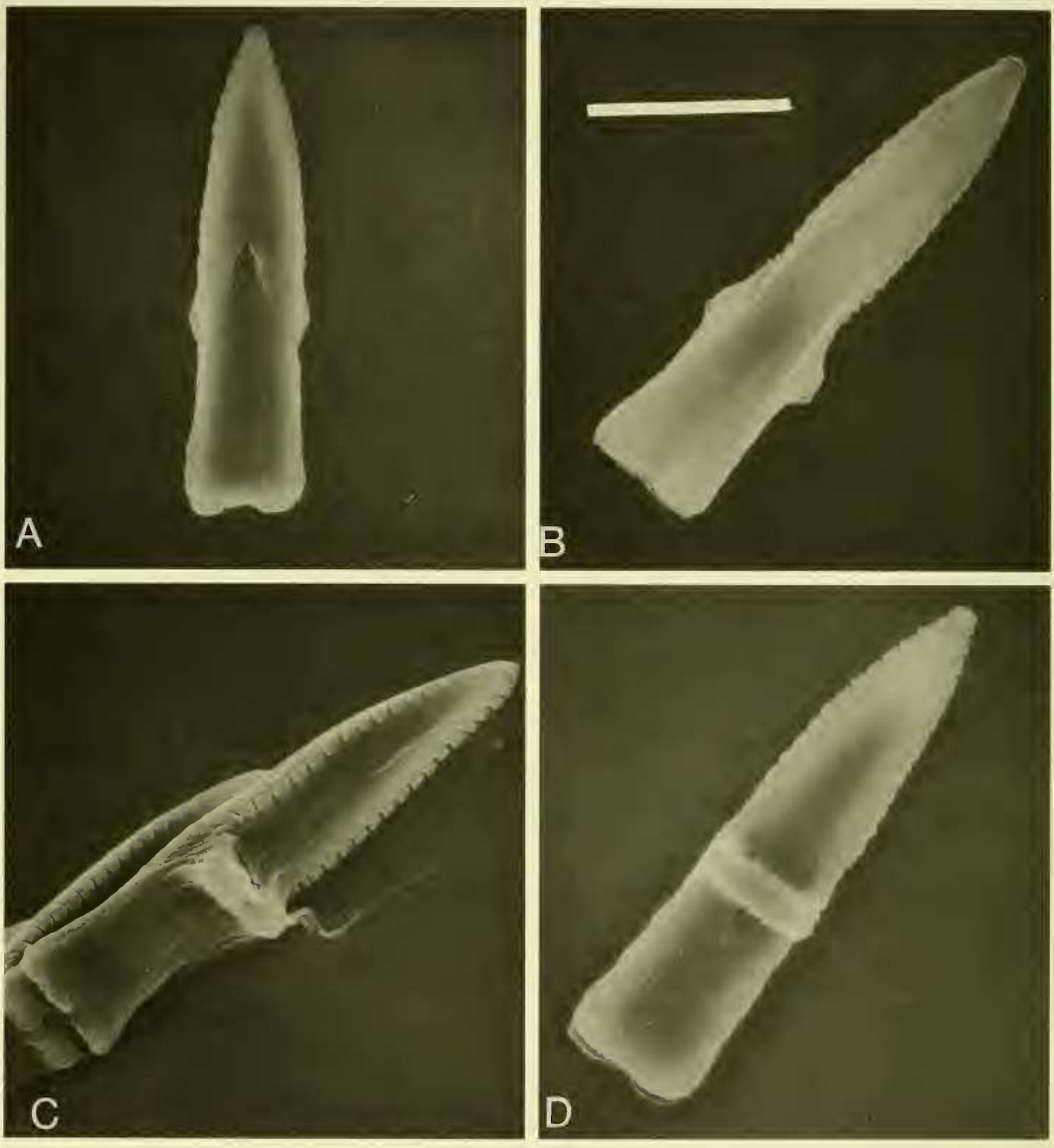

FIGURE 5. Radular teeth of specimen with color typical of *T. ratna*. A, B. Dorsal view of tooth of specimen from Palau, CASIZ 099058. A. scale = 15 μm. B. scale = 7.5 μm. C. Ventral view of tooth of specimen from Borneo, CASIZ 078470, scale = 15 μm. D. Ventral view of tooth of specimen from Palau, CASIZ 099058, scale = 10 μm.

Guinea (CASIZ 072919) examined had faint blue markings on the parapodia and head, but lacked any trace of blue on the foot. Another specimen from Australia (CASIZ 071469) and the specimen from the Maldives illustrated by Yonow (1994), had faint blue lines on the parapodia, but lacked any trace of blue on the head or foot. One specimen having no trace of blue markings has been found in the Indian Ocean (Yonow, 1994). Only a single specimen having coloration similar to *T. ratna* has been found from the western Indian Ocean. *Thuridilla*

ratna is considered uncommon in Western Australia (Wells and Bryce, 1993) and, together with Jensen's (1992) record from Thailand, represents the only other record of this color form from the Indian Ocean.

Internally, there is little difference between *Thuridilla bayeri*, *T. ratna* and *T. splendens*. All three have paired lateral vessels from the pericardium and posterior vessels that originate from a common junction with the pericardium. There are fewer lateral branches in most specimens with the color pattern of *T. bayeri*, though there is considerable overlap in branching pattern with specimens typical of *T. ratna* and *T. splendens*. Jensen (1992) indicated that there are slight differences in the size of the pharyngeal pouch and shape of the radular teeth between *T. bayeri* and *T. ratna*. No consistent differences in the relative proportions of the muscular buccal mass and pharyngeal pouch and the shape and size of the radular teeth could be determined in the present material, with one exception. The pharyngeal pouch of *T. splendens* is slightly larger proportionately than the pouch of *T. bayeri* and *T. ratna*. The configuration of the reproductive system, including the shape of the bursa copulatrix and penial papilla, is virtually identical in the specimens typical of *T. bayeri*, *T. ratna* and *T. splendens* examined in this study.

Color photographs of more than 50 specimens of *Thuridilla bayeri* and *T. ratna* from a broad geographical area were compared in detail. No consistent difference in pattern could be discerned. The fact that some specimens had faint blue markings on the parapodia and entirely lacked blue markings on the head and foot, suggests that they are intermediate in coloration between that described for the two species. No consistent anatomical differences could be found in branching of the dorsal vessels, morphology of the buccal mass, radula or reproductive system that could be correlated with differences in coloration. All of these data strongly suggest that the described differences between *T. bayeri* and *T. ratna* are simply variation within a single species that is extremely variable in its coloration. Johnson and Boucher (1983) noted that the egg capsule size of *T. bayeri* and *T. ratna* was somewhat different. Possible developmental differences of the two color forms require further investigation. On this basis, *Thuridilla ratna* is regarded as a junior synonym of *T. bayeri*. Both species were described in the same paper (Marcus, 1965), but *T. bayeri* appears first in the text and is, therefore, regarded as the senior synonym.

As noted above, specimens of *Thuridilla splendens* are similar in coloration and internal anatomy to *T. bayeri*. However, specimens of *T. splendens* are consistently different in that they have yellow spots on the sides of the parapodia and foot which are absent in all variants of *T. bayeri*. In addition, the pharyngeal pouch is somewhat proportionately larger in *T. splendens*. On these bases, *T. splendens* is regarded as distinct from *T. bayeri*.

2. Thuridilla lineolata (Bergh, 1905)

Elysia? lineolata Bergh, 1905: 85, pl. 3, fig. 10, pl. 13, figs. 25, 26.
Thuridilla lineolata (Bergh) Jensen, 1992: 277.

MATERIAL EXAMINED. — CASIZ 070285, one specimen, Manado, Sulawesi, Indonesia, 0.5 m depth, 21 May 1989, Pauline Fiene-Severns. CASIZ 099059, two specimens, one dissected, Bunaken Island, Manado, Sulawesi, Indonesia, 3 m depth, 20 May 1990, Pauline Fiene-Severns.

DISTRIBUTION. — This species is known only from Indonesia (Bergh, 1905; present study).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 1D) are light blue. The edge of the parapodia is lined with a band of bright orange. Immediately inside this band is a narrower black band. Two black lines and an orange band are present at the base of the parapodia, as well. There is a narrow black band surrounding the head, near the level of the eyes. A v-shaped black band is near the middle of each rhinophore and the rhinophores are tipped with orange. Orange pigment is present on the anterior margin of the foot.

PERICARDIUM AND DORSAL VESSELS (Fig. 6A). — There are paired lateral and posterior vessels. These vessels are thin compared to most other species. The anterior vessels are bifurcate near their tips. The more posterior vessels have separate origins from the pericardium and give rise to one or two short branches.

BUCCAL MASS AND RADULA. — The buccal mass (Fig. 6B, C) contains a large pharyngeal

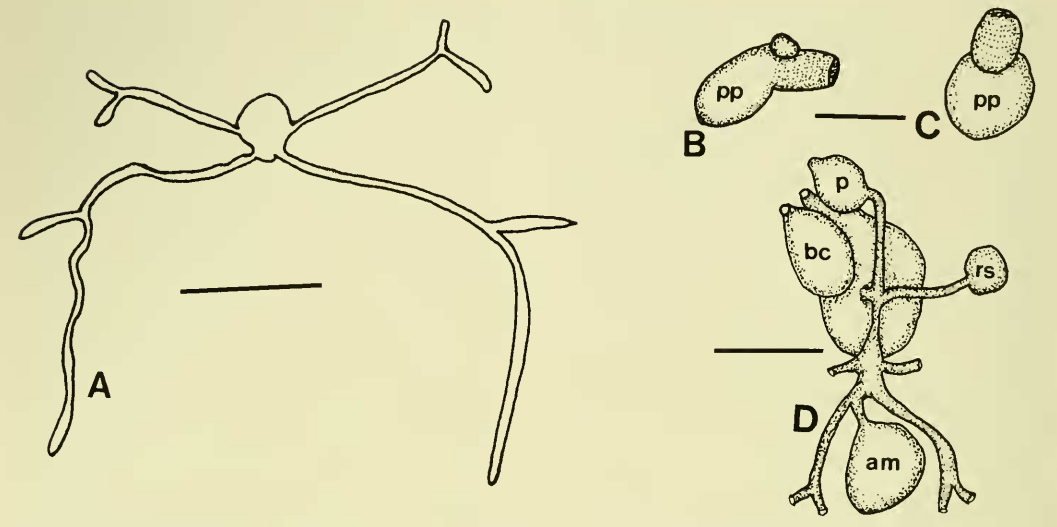

FIGURE 6. *Thuridilla lineolata* (Bergh, 1905). A. Branching of pericardial vessels, scale = 4.0 mm. B. Lateral view of buccal mass. C. Ventral view of buccal mass. B., C. pp = pharyngeal pouch, scale = 0.25 mm. D. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 0.5 mm.

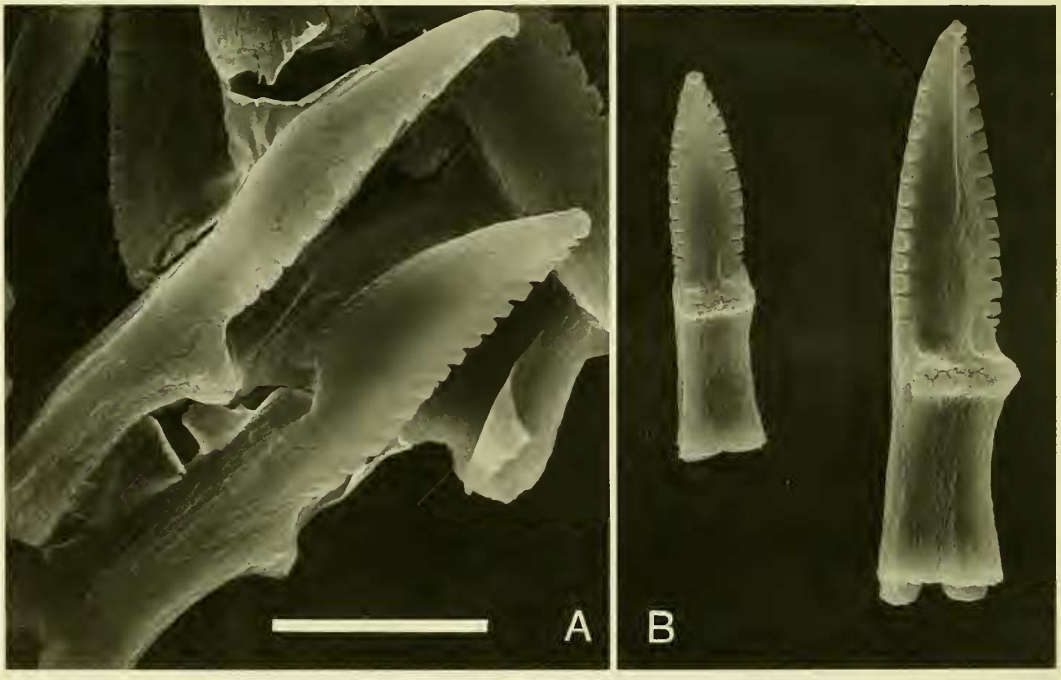

FIGURE 7. *Thuridilla lineolata* (Bergh, 1905). Radular teeth. A. Lateral view of specimen from Indonesia, CASIZ 099059, scale = 10 μm. B. Ventral view of same, scale = 15 μm.

pouch and a smaller muscular portion of the buccal mass. The radula contains 17 teeth (8 ventral teeth and 9 dorsal) with another 17 teeth in the ascus. The teeth (Fig. 7) bear 12–16 denticles.

REPRODUCTIVE SYSTEM (Fig. 6D). — The ovotestis, prostate and albumen glands are arranged as in *T. bayeri*. The ampulla enters the female gland mass anterior of the right hermaphroditic duct near its junction with the left hermaphroditic duct. A small spherical receptaculum seminis joins the large female gland mass by means of thin, elongate duct. The bursa copulatrix is thin and pyriform and exits near the female gonopore. The vas deferens branches from the female gland mass and enters the small, conical, unarmed penial papilla.

DISCUSSION. — This species has not been recorded since its original description (Bergh, 1905). Bergh figured this species in a color plate. The pattern of coloration he illustrated is identical to that found in the present material. There is no doubt that the present material is conspecific with Bergh's.

Eliot (1906: 689), in reviewing the status of Kelaart's Ceylonese nudibranchs, stated that *Elysia caerulea* Kelaart, 1858 "can hardly be anything but *Elysia lineolata* of Bergh, which has a similarly gorgeous coloration, though there are some differences in detail. For instance, in Kelaart's animal the rhinophores have not red tips, but a red ring below a black tip."

While Eliot was fairly certain that *T. lineolata* should be regarded as a junior synonym of *T. caerulea*, the differences in coloration between the two, though minor, appear consistent.

Another animal depicted by Wells and Bryce (1993: fig. 75) as *T.* sp. has similar coloration, but with more black pigment relative to orange and blue. It also appears to be distinct from either *T. lineolata* or *T. caerulea*. Pending detailed study of specimens from western Australia and Sri Lanka, it is preferable to retain *T. lineolata* as distinct from *T. caerulea*.

Morphologically, *T. lineolata* appears to be most closely related to *T. undula* sp. nov. The two differ in color, with *T. undula* having an undulating, orange parapodial marginal band, while the orange marginal band of *T. lineolata* is straight.

In *T. lineolata*, the lateral pericardial vessels are much less branched than in *T. undula* and the posterior vessels join the pericardium separately rather than from a common connection.

3. Thuridilla livida (Baba, 1955)

Elysia livida Baba, 1955: 12, fig. 13, pl. 4, fig. 10; Carlson and Hoff, 1978: 100, figs. 10c, d, 13; Gosliner, 1987: 53, fig. 44.

Thuridilla livida (Baba), Jensen, 1992: 277.

MATERIAL EXAMINED. — SAM A35280, one specimen, Mbibi, Sodwana Bay National Park, Natal, South Africa, 1 m depth, 6 May 1982, T. M. Gosliner. SAM A35271, one specimen, Adlams Reef, Sodwana Bay National Park, Natal, South Africa, 1 m depth, 7 May 1982, T. M. Gosliner. SAM A35272, one specimen, dissected, Mbibi, 2 m depth, 10 May 1982, T. M. Gosliner. CASIZ 074211, two specimens, Passe Femme, Aldabra Atoll, Seychelles, 2 m depth, 23 March 1986, T. M. Gosliner. CASIZ 070022, one specimen, radula removed, 1 km wnw of Onna Village, Horseshoe Cliffs, 3 m depth, 16 July 1989, R. F. Bolland.

DISTRIBUTION. — Enewetak, Marshall Islands (Johnson and Boucher, 1983), Okinawa (present study), Japan (Baba, 1955), Guam (Carlson and Hoff, 1978), Aldabra Atoll (present study), South Africa (Gosliner, 1987).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 1C) are dark brown to black. The parapodia are lined with a series of longitudinal lines. The innermost line is black followed by lines of orange, black and bright blue. The head and rhinophores are black. The apical half of the rhinophores has varying amounts of opaque white pigment. Black, orange and blue lines are also present along the anterior margin of the foot.

PERICARDIUM AND DORSAL VESSELS (Fig. 8A–C). — The branching of the vessels was examined in three specimens. In two animals, there is only a single pair of posterior vessels with separate origins from the pericardium. In the third specimen, there is a second pair of lateral vessels. The lateral vessels are bifurcate. The posterior vessels may be unbranched or may have a few short branches.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 8D) is slightly larger than the muscular portion of the buccal mass. The radula consists of 28 teeth (8 in a coil, 13 in the ventral limb and 7 in the dorsal limb). The

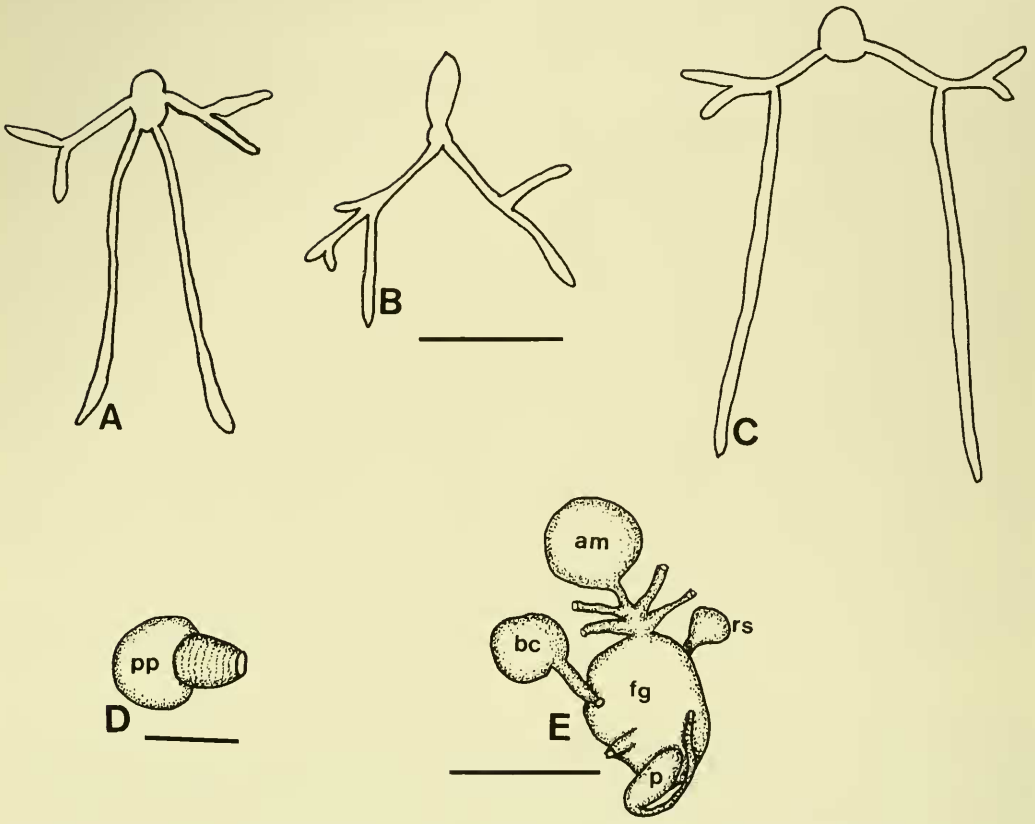

FIGURE 8. *Thuridilla livida* (Baba, 1955). A–C. Branching of pericardial vessels, scale = 4.0 mm. D. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25 mm. E. Distal reproductive organs: am = ampulla, bc = bursa copulatrix, fg = female gland mass, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

teeth (Fig. 9) are triangular with a short base and longer cutting edge. The cutting edge contains approximately 15 coarse denticles per side. The denticles continue as distinct striations on to the dorsal surface of the teeth.

REPRODUCTIVE SYSTEM (Fig. 8E). — The diffuse ovotestis are identical to those described for *T. bayeri*. The ampulla is large and spherical. It enters the female gland mass immediately posterior to the ducts from the ovotestis, albumen and prostate glands. The female gland mass is large and irregular in shape. A spherical receptaculum seminis enters the gland mass via a short duct. The spherical bursa copulatrix exits from its own gonopore immediately posterior to the female gonopore, by means of an elongate duct. The vas deferens leads to the simple, ovoid, unarmed penial papilla.

DISCUSSION. — In their discussion of *Thuridilla livida*, Carlson and Hoff (1978) described the existence of a distinct species similar in coloration to *T. livida* and noted radular differences between the two. *Thuridilla livida* is most closely related to this species described here as *T. hoffae* sp. nov. and more distantly to other species with orange and blue parapodial markings. In addition to having this color pattern, all members of this species complex have prominent striations on the teeth that extend from the denticles to the dorsal surface of the tooth. The differences between *T. livida* and *T. hoffae* in coloration described by Carlson and Hoff are consistent in the present material. Principally, *T. livida* has a distinct narrow iridescent blue submarginal line while *T. hoffae* has a se-

FIGURE 9. *Thuridilla livida* (Baba, 1955). Lateral view of radular teeth of specimen from South Africa, SAM A35272, scale = 10 μm.

ries of iridescent blue to blue green patches. *T. livida* has orange and blue lines on the anterior margin of the foot that are absent in *T. hoffae*. The general body color is darker in *T. hoffae* than in *T. livida*.

Carlson and Hoff stated that the radular teeth of *T. livida* are wider and more finely denticulate than those of *T. hoffae*. Those differences are also evident and consistent in the present material.

In addition to the color and radular differences described by Carlson and Hoff, other anatomical features differ between the two species. In *T. livida*, the two posterior vessels enter the pericardium separately, while in *T. hoffae* they have a common junction. The pharyngeal pouch of *T. livida* is proportionately smaller than that of *T. hoffae*, while the penial papilla is wider and less acute than that of *T. hoffae*.

4. Thuridilla moebii (Bergh, 1888)

Plakobranchus? moebii Bergh, 1888: 759, pl. 78, fig. 19.
Elysia moebii (Bergh) Gosliner, 1987: 53, fig. 42.
Thuridilla moebii (Bergh) Jensen, 1992: 277; Wells and Bryce, 1993: 67, fig. 74.

MATERIAL EXAMINED. — SAM A52166, one specimen, dissected, Mbibi, Sodwana Bay National Park, Natal, South Africa, 17 May 1981, T. M. Gosliner.

DISTRIBUTION. — Western Australia (Wells and Bryce, 1993), Mauritius (Bergh, 1888), Reunion Island and South Africa (Gosliner, 1987).

EXTERNAL MORPHOLOGY. — The body is bluish green (Fig. 1F). At the margin of the parapodia is an orange longitudinal band. Below this band is a black band. Both bands are covered with minute opaque white spots. The head is the same color as the rest of the body. The rhinophores and anterior margins of the foot contain the same sequence of orange and black pigment with white spotting as the parapodia.

PERICARDIUM AND DORSAL VESSELS. — The branching of the dorsal vessels could not be determined, owing to poor preservation of the single specimen.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 10A) is massive relative to the muscular portion. The radula contains 23 teeth (7 in the ascus, 8 in the ventral limb and 8 in the dorsal limb). The teeth (Fig. 11) bear approximately 18 coarse denticles on either side. The basal portion of the tooth is slightly shorter than the cutting portion.

REPRODUCTIVE SYSTEM (Fig. 10B). — The diffuse ovotestis is identical to that described for *T. bayeri*. The ampulla is large and spherical. It enters the female gland mass immediately posterior to the ducts from the ovotestis, albumen and prostate glands. The female gland mass is large and ovoid. The spherical receptaculum seminis enters the gland mass via a short duct. The spherical bursa copulatrix exits from its own gonopore immediately posterior to the female gonopore, by means of an extremely short duct. The short vas deferens leads to the simple, blunt, unarmed penial papilla.

DISCUSSION. — *Thuridilla moebii* is only known from four specimens, one each collected from Mauritius, Reunion Island, South Africa and the Houtman Abrolhos Islands off western Australia. Its color pattern is quite distinctive with a blue to greenish ground color and a burnt orange marginal band with scattered opaque white spots. It is a member of the clade of spe-

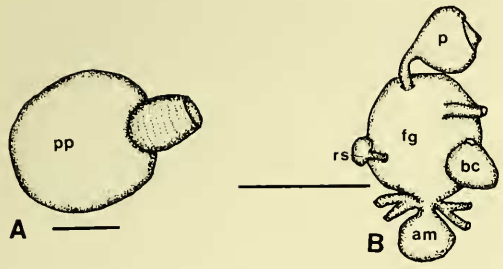

FIGURE 10. *Thuridilla moebii* (Bergh, 1888). A. Ventral view of buccal mass, pp= pharyngeal pouch, scale= 0.11 mm. B. Distal reproductive organs: am= ampulla, bc= bursa copulatrix, fg= female gland mass, p= penis, rs= receptaculum seminis, scale= 1.0 mm.

FIGURE 11. *Thuridilla moebii* (Bergh, 1888). Lateral view of radular tooth of specimen from South Africa, SAM A52166, scale= 15 μm.

cies that has an expanded pharyngeal pouch, and differs markedly from all other members of the clade by its distinct coloration. It differs from all members of the genus in its possession of a short, bulbous penial papilla. Details of the branching of the pericardial vessels remain unknown, owing to the poor preservation of the single specimen available.

5. Thuridilla splendens (Baba, 1949)

Elysia splendens Baba, 1949: 36, fig. 28, pl. 10, fig. 32.

Elysia sp. Willan and Coleman, 1984: 4, unnumbered figure.

Thuridilla splendens (Baba) Jensen, 1992: 277.

MATERIAL EXAMINED. — CASIZ 074697, one specimen, dissected, Seragaki Beach, 1.3 km ene of Maeki-zake, Okinawa, Ryukyu Islands, 3 m depth, 31 August 1989, R. F. Bolland. CASIZ 069993, one specimen, 2 km e of Oguma-saki, Okinawa, intertidal, 16 March 1987, R. F. Bolland. CASIZ 099060, two specimens, one specimen with radula removed, Tengan, Okinawa, 3 m depth, 5 March 1994, R. F. Bolland.

DISTRIBUTION. — Japan (Baba, 1949), Okinawa (present study), Guam (Carlson and Hoff, pers. comm.), Australia (Willan and Coleman, 1984 as *Elysia* sp.).

EXTERNAL MORPHOLOGY. — The body (Fig. 1E) is dark brown with a series of complete and interrupted bright yellow lines or series of spots. The margin of the parapodia consists of a red longitudinal band. Below this band is a black band with yellow spots. Below this band is a series of light blue ovoid spots. Often one or two additional series of spots are present below this level. The head has a whitish or blue mark. The rhinophores are black with yellow pigment basally and red apices. The anterior margins of the foot also have red, black with yellow spots, and blue pigment.

PERICARDIUM AND DORSAL VESSELS. — Branching of the vessels was observed in three specimens (Fig. 12A–C). Both lateral and posterior vessels are present. The lateral vessels are simple or bifurcate near their tips. The posterior vessels have a common origin from the pericardium with elongate posterior extensions. These posterior vessels have two undivided branches emanating from the primary vessels.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 12D) is larger than the more anterior muscular portion. The radula consists of 20 teeth (9 in the ventral limb, 6 in the dorsal limb and 5 in the ascus). The teeth (Fig. 13) are triangular with the cutting portion being slightly longer than the basal one. There are 14–18 coarse denticles along either side of the cutting margin.

REPRODUCTIVE SYSTEM (Fig. 12E). — The ovotestis, albumen and prostate glands are diffusely arranged as described for *T. bayeri*. The ampulla is spherical and joins with the ducts

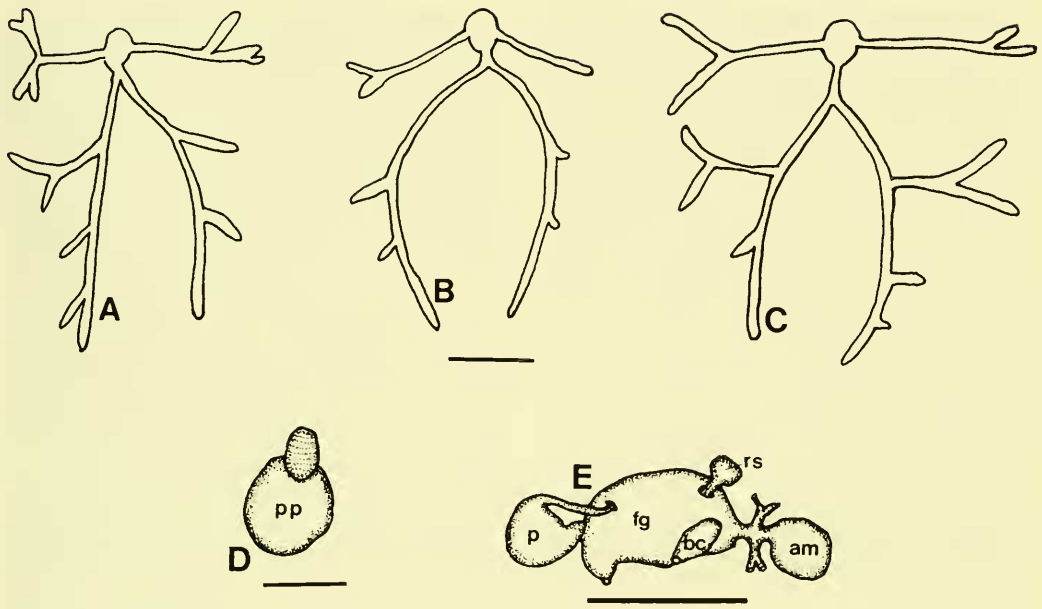

FIGURE 12. *Thuridilla splendens* (Baba, 1949). A–C. Branching of pericardial vessels, scale = 5.0 mm. D. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25 mm. E. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, fg = female gland mass, p = penis, rs =r eceptaculum seminis, scale = 1.0 mm.

from the ovotestis, albumen and prostate glands prior to entering the female gland mass. The spherical receptaculum seminis enters the posterior portion of the female gland mass, via a short duct. The pyriform bursa copulatrix exits, by means of its own gonopore, via a short duct. The vas deferens enters the penis. The unarmed penial papilla is curved and rounded. It exits adjacent to the female gonopore.

DISCUSSION. — The anatomy of this species and its similarity to *T. bayeri* and its junior synonym, *T. ratna*, are discussed in the discussion of *T. bayeri*. *Thuridilla splendens* is distinguished from *T. bayeri* by the yellow spots on the parapodia and foot and the expanded pharyngeal pouch.

6. **Thuridilla vatae** (Risbec, 1928)

Elysia vatae Risbec, 1928: 281, pl. 12, fig. 7; Carlson and Hoff, 1978: 108, figs 5c, 16f, g, 19; Gosliner, 1987: 53, fig. 43.

Thuridilla vatae (Risbec) Jensen, 1992: 273, figs. 14d, 16j–l, 18d.

MATERIAL EXAMINED. — SAM A35275, one specimen, Adlam's Reef, Sodwana Bay National Park, Natal, South Africa, 9 May 1982, T. M. Gosliner. CASIZ 073388, one specimen, Cement Mixer Reef, Madang Lagoon, Madang, Papua New Guinea, 2 m depth, 22 October 1986, T. M. Gosliner. CASIZ 070008, one specimen, Horseshoe Cliffs, 1 km, wnw of Onna Village, Okinawa, Ryukyu, Islands, 3 m depth, 16 July 1989, R. F. Bolland. CASIZ 088076, one specimen, 3 km e of Lighthouse near Dakak Resort, Mindanao, Philippines, 1 April 1993, T. M. Gosliner. CASIZ 065280, one specimen, barrier reef pinnacle, n. of Pig Island, Madang Lagoon, Papua New Guinea, 5 m. depth, 25 January 1988, J. Mizeu. CASIZ 065281, the Quarry, 1 km s of Cape Croiselles, Madang Province, Papua New Guinea, 4 m depth, 11 February 1988, J. Mizeu. CASIZ 065310, one specimen, Cement Mixer Reef, Madang Lagoon, Papua New Guinea, 19 January 1988, R. C. Willan. CASIZ 065337, one specimen, Rempi Lagoon, 20 km n of Madang, Papua New Guinea, 15 m depth, 3 February 1988, R. C. Willan. CASIZ 065349, one specimen, radula removed, the quarry, 1 km s of Cape Croiselles, Madang Province, Papua New Guinea, 11 February 1988, R. C. Willan. CASIZ 073030, one specimen, jetty, Christensen Research Institute, Madang Lagoon, Papua New

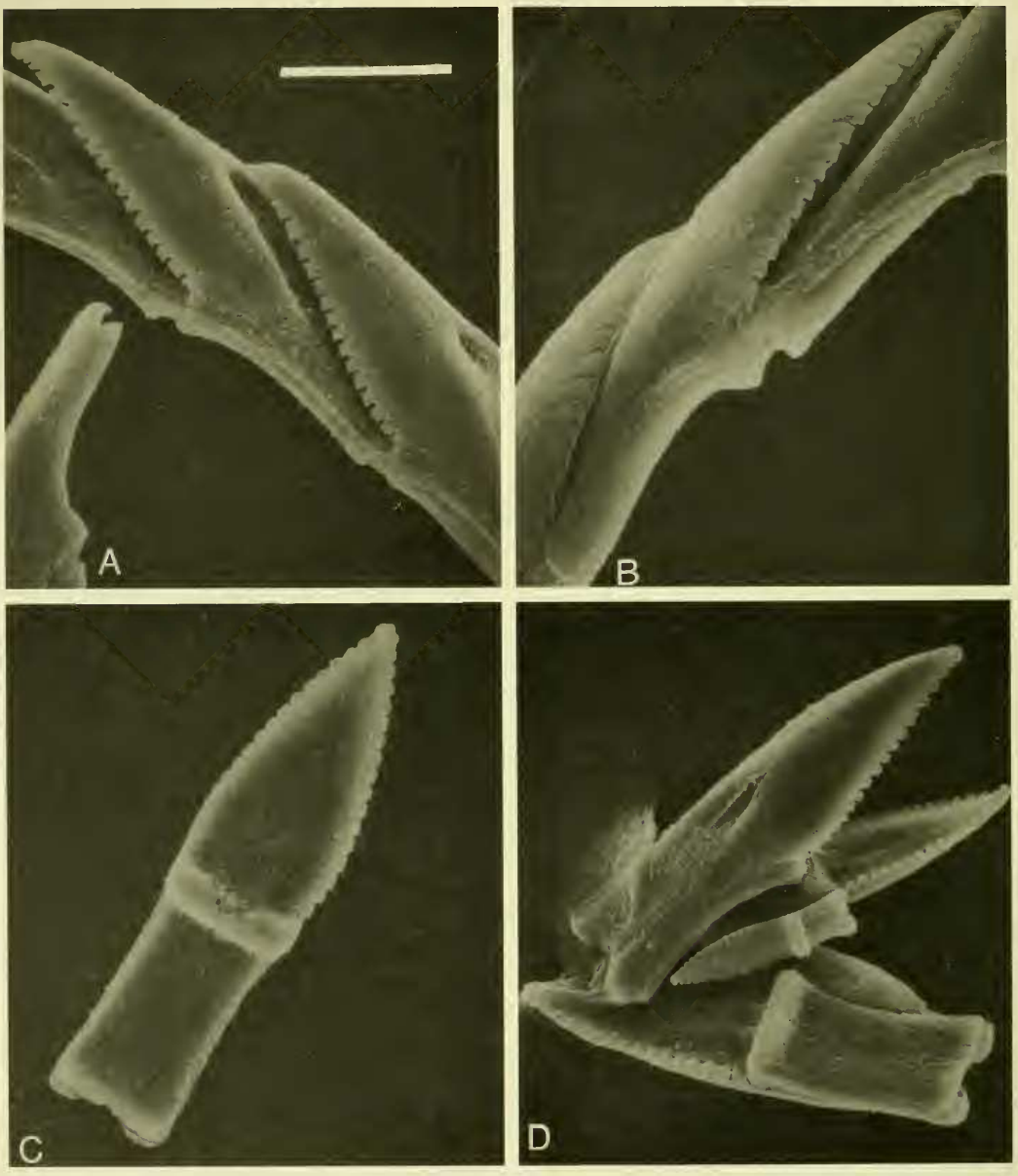

FIGURE 13. *Thuridilla splendens* (Baba, 1949). Radular teeth of specimen from Okinawa CASIZ 099060. A. Dorsolateral view, scale = 20 μm. B. Lateral view, scale = 10 μm. C. Ventral view, scale = 15 μm. D. Teeth from ascus, scale = 20 μm.

Guinea, 30 September, 1986, T. M. Gosliner. CASIZ 087158, one specimen, dissected, 2 km s of St. Gilles, Reunion, 2 m depth, 27 July 1977, M. L. Gosliner. CASIZ 099061, one specimen, dissected, Wongat Wall, Madang Lagoon, Madang, Papua New Guinea, 10 m depth, 30 August 1989, T. M. Gosliner. CASIZ 099062, one specimen, Bunaken Island, Manado, Sulawesi, Indonesia, under rock, 1.5 m depth, 20 May 1990, P. Fiene-Severns.

DISTRIBUTION. — New Caledonia (Risbec, 1928), Guam, Palau and Maug (Carlson and Hoff, 1978), Marshall Islands (Johnson and Boucher, 1983, Johnson, pers. comm.), Western

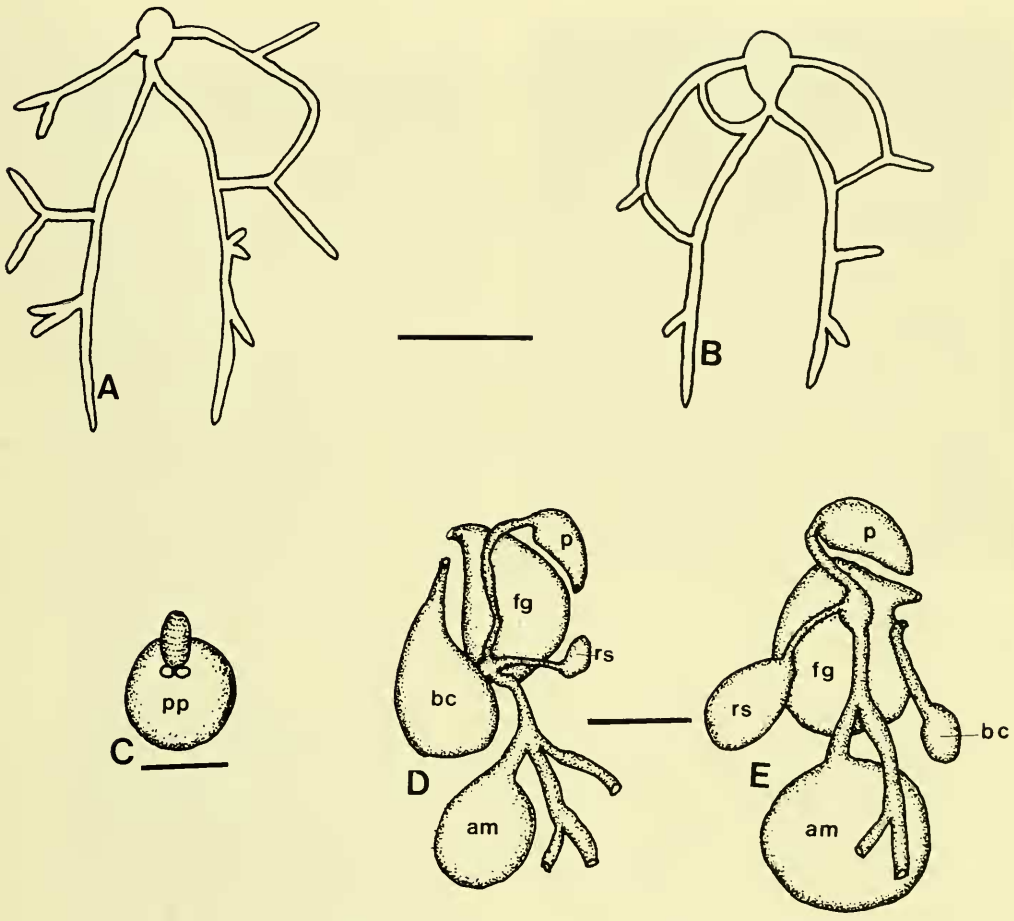

FIGURE 14. *Thuridilla vatae* (Risbec, 1928). A, B. Branching of pericardial vessels, scale = 4.0 mm. C. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25mm. D. Ventral view of distal reproductive organs, CASIZ 099061, Papua New Guinea. E. Distal reproductive organs, CASIZ 087158, Reunion Island. D., E. am = ampulla, bc = bursa copulatrix, fg = female gland mass, p = penis, rs = receptaculum seminis, scale = 0.5 mm.

Australia (Jensen, 1992), Indonesia (present study), Papua New Guinea (present study), Philippines (present study), Reunion Island (present study), Aldabra Atoll (present study), South Africa (Gosliner, 1987).

EXTERNAL MORPHOLOGY. — The body (Fig. 16A) is dark bluish with scattered black and yellow spots. The margin of the parapodia is cream to yellow, but this pigment does not form a distinct band as in other members of the genus. The head is the same color as the body with a y-shaped yellowish or white marking that extends onto most of the length of the rhinophores. The apex of the rhinophores is bright red. The anterior margin of the foot is the same color as the remainder of the body.

PERICARDIUM AND DORSAL VESSELS (Fig. 14 A, B). — Both lateral and posterior vessels are present. The lateral vessels are bifurcate for much of their length. The posterior vessels have a common origin with the pericardium and have a series of 2–3 bifurcate or undivided secondary branches. The right anteriormost branch is connected with the more posterior branch of the right lateral vessel.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 14C) is massive relative to the muscular portion. The radula consists of 22

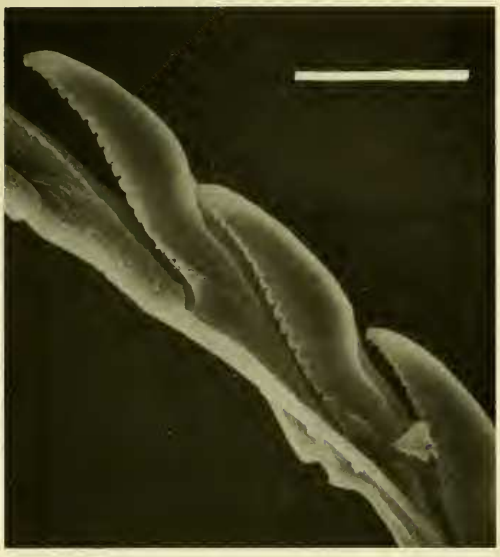

FIGURE 15. *Thuridilla vatae* (Risbec, 1928. Radular teeth. A. Lateral view of specimen from Papua New Guinea, CASIZ 099061, scale = 15 μm.

teeth (14 in the ventral limb, 8 in the dorsal limb and none present in the ascus). The radular teeth (Fig. 15) are triangular with 16–17 coarse denticles along either side of the cutting margin of the tooth. The basal portion is approximately equal in length to the cutting portion.

REPRODUCTIVE SYSTEM (Fig. 14D, E). — The arrangement of the diffuse ovotestis, albumen and prostate glands is identical to that described for *T. bayeri*. The ducts from these glands join the spherical ampulla and enter the female gland mass near the small membrane gland, situated near the posterior end of the large mucus gland. From this junction, the vas deferens emerges and enters the acutely pointed, unarmed penis. The spherical receptaculum seminis joins the female gland mass via an elongate duct. The pyriform bursa copulatrix is variable in size, but when fully developed, is as large as the female gland mass. It exits via its own gonopore, immediately posterior to the female gonopore. In the specimen from Reunion, it was minute, whereas in a specimen from Papua New Guinea, it was almost the same size as the female gland mass.

DISCUSSION. — *Thuridilla vatae* is most similar to *T. albopustulosa* sp. nov. Both species are unique among species of *Thuridilla* in having connections between the lateral and posterior pericardial vessels. The radular teeth of *T. vatae* appear to be more finely denticulate than those of *T. albopustulosa*. The penial papilla of one specimen of *T. albopustulosa* has a constriction in the middle of its length. At present, it is not known whether this is a consistent difference between the two species.

Aspects of the coloration of *T. vatae* differ consistently from that of *T. albopustulosa*. In *T. vatae*, the ground color is a dark gray to black while that of *T. albopustulosa* is blue. The parapodia of *T. vatae* are ornamented with black and yellow spots, while those of *T. albopustulosa* are white or cream. In *T. vatae*, white pigment covers most of the length of rhinophores and only the apex is red. In *T. albopustulosa*, the majority of the rhinophores are red rather than white. In *T. vatae*, the red pigment is a solid transverse band, while in *T. albopustulosa* the red is a diagonal band with white patches within the band.

7. Thuridilla virgata (Bergh, 1888)

Plakobranchus virgatus Bergh, 1888: 758, pl. 77, fig. 8, pl. 78, figs. 20–22.
Elysia virgata (Bergh) Gosliner, 1987: 52, fig. 41.
Thuridilla virgata (Bergh) Jensen, 1992: 277.

MATERIAL EXAMINED. — SAM A35274, six specimens, one dissected, one with radula removed, Mbibi, Sodwana Bay National Park, Natal, South Africa, 1–2 m depth, 6 May 1981, T. M. Gosliner. CASIZ 073973, one specimen, Mbibi, Sodwana Bay National Park, Natal, South Africa, 2 m depth, 18 May 1981, T. M. Gosliner. CASIZ 070336, one specimen, dissected, 2 km wsw of Mora Mora Resort, Ifaty, 20 km n. of Tulear, Madagascar, 3 m depth, 9 April 1989, T. M. Gosliner. CASIZ 102280, one specimen, Ras Nungwi, Zanzibar, Tanzania, 1 m depth, 6 November, 1994, T. M. Gosliner.

DISTRIBUTION. — Mauritius (Bergh, 1888), Madagascar (present study), South Africa (Gosliner, 1987), Tanzania (present study).

EXTERNAL MORPHOLOGY. — The body is blue to blue green (Fig. 16B). A series of broad, black longitudinal markings are present on the parapodia. The parapodial margin is the same color blue as the remainder of the body. The head is blue with black markings. A white

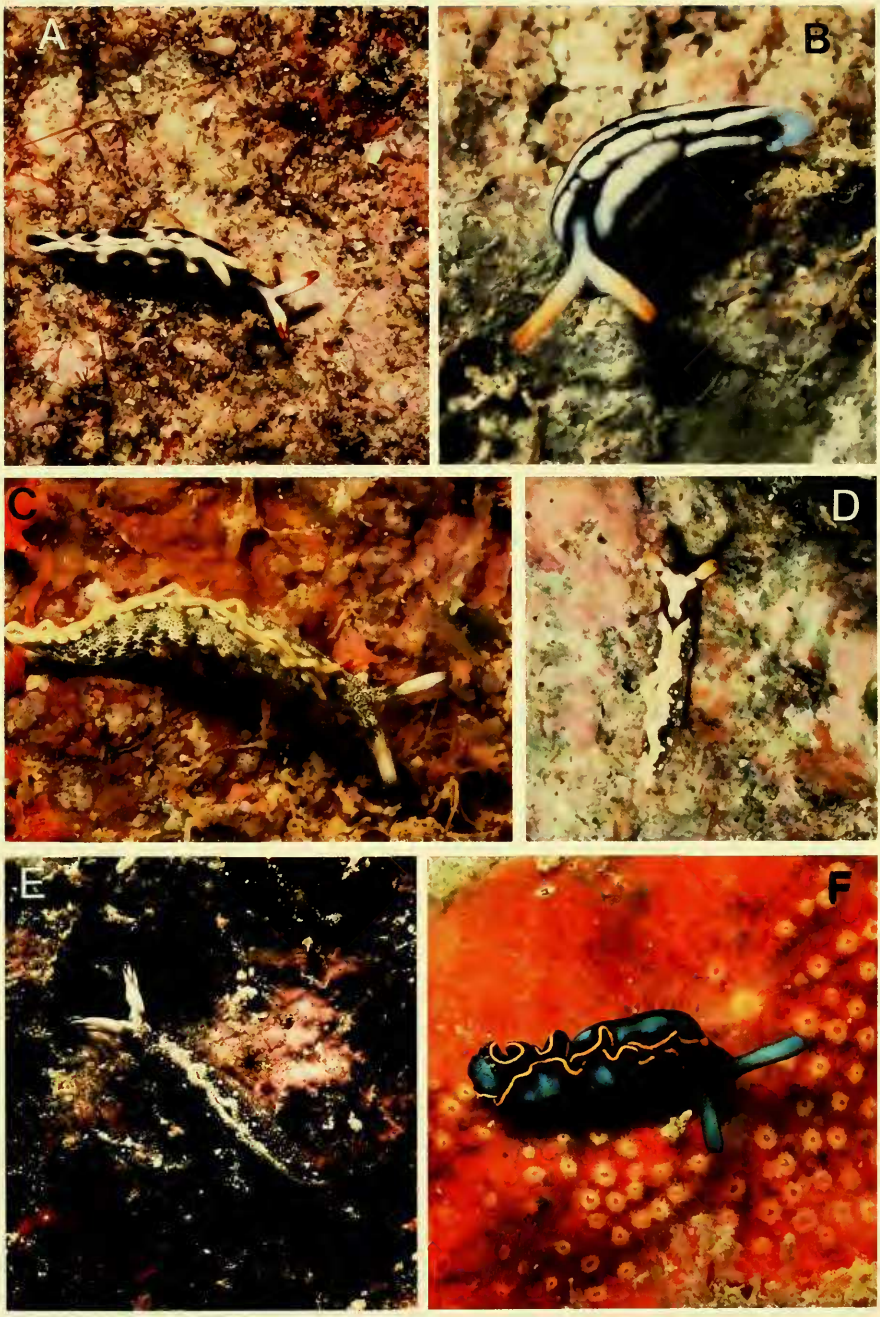

FIGURE 16. Living animals. A. *Thuridilla vatae* (Risbec, 1928), Madang, Papua New Guinea, 11 mm in length. B. *Thuridilla virgata* (Bergh, 1888), Tulear, Madagascar, 18 mm in length. C. *Thuridilla carlsoni* sp. nov., Madang, Papua New Guinea, 20 mm in length. D. *Thuridilla kathae* sp. nov., Tulear, Madagascar, 9 mm in length. E. *Thuridilla flavomaculata* sp. nov., Manado, Sulawesi, Indonesia, 11 mm in length, photo by Pauline Fiene-Severns. F. *Thuridilla hoffae* sp. nov, Madang, Papua New Guinea, 13 mm in length.

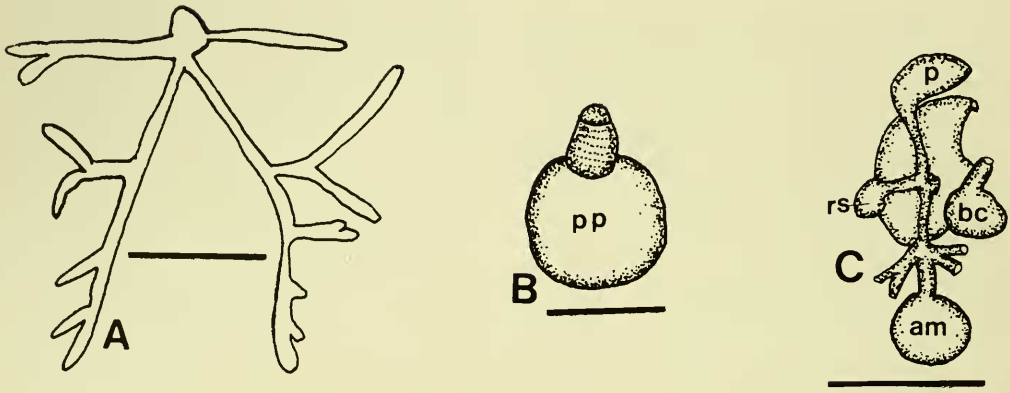

FIGURE 17. *Thuridilla virgata* (Bergh, 1888). A. Branching of pericardial vessels, scale = 4.0 mm. B. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25mm. C. Distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

marking extends from the anterior portion of the head to the base of the rhinophores. The apical two-thirds of the rhinophores is orange. The anterior margins of the foot are black.

PERICARDIUM AND DORSAL VESSELS (Fig. 17A). — Paired lateral and posterior vessels are present. The lateral vessels are undivided or bifurcate at their tips. The posterior vessels have a common insertion with the pericardium. They give rise to 3–4 undivided or secondary vessels on either side.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 17B) is much larger than the muscular portion of the buccal mass. The radula of one specimen examined contained 20 teeth, with 11 in the ventral limb, 7 in the dorsal one and 3 in the ascus. The teeth (Fig. 18) bear 18–20 coarse denticles along the cutting margin. The basal portion of the tooth is approximately equal in length to the cutting portion.

REPRODUCTIVE SYSTEM (Fig. 17C). — The ovotestis, albumen and prostate glands are diffuse and occupy much of the tissue within the parapodia and are identical in form to that described for *T. bayeri*. Their ducts join the duct from the spherical ampulla and collectively enter the female gland mass. The small, spherical receptaculum seminis joins the female gland mass near the junction of the ampulla and associated ducts, by means of a short duct. The larger bursa copulatrix has a short duct that has its own gonopore. The vas deferens emerges from the junction of the ampulla and receptaculum seminis with the female gland mass. It continues anteriorly and enters the end of the simple unarmed penis.

DISCUSSION. — *Thuridilla virgata* has a blue body with black parapodial bands and orange pigment on the rhinophores. This color pattern clearly distinguishes it from all other members of the genus. Morphologically, *T. virgata* is most closely related to *T. vatae*, *T. albopustulosa* and *T. moebii*. All of these species have an expanded pharyngeal pouch and a bluish body color. The duct of the receptaculum seminis appears shorter in *T. virgata* than in these other closely related species.

8. Thuridilla carlsoni sp. nov.

Elysia gracilis Carlson and Hoff, 1978, not Risbec, 1928: 95, figs. 6d, e, 8.
Thuridilla sp. Wells and Bryce, 1993: 67, fig. 71.

TYPE MATERIAL. — Holotype: CASIZ 075939, one specimen, the Quarry, 1 km s. of Cape Croiselles, Madang Province, Papua New Guinea, 28 November 1990, T. M. Gosliner.

Paratypes: CASIZ 078542, two specimens, under rock, Bunaken Island, Manado, Sulawesi, Indonesia, 3 m depth, 5 May 1991, P. Fiene-Severns. CASIZ 076447, four specimens, Hekili Point, Maui, Hawai-

FIGURE 18. *Thuridilla virgata* (Bergh, 1888). Radular teeth. A. Lateral view of tooth, CASIZ 07336, Madagascar, scale = 15 μm.

ian Islands, 1 m depth, October 1990, C. Pittman. CASIZ 065784, two specimens, one dissected, the quarry, 1 km s. of Cape Croiselles, Madang Province, Papua New Guinea, 2 m depth, 11 February 1988, T. M. Gosliner. CASIZ 086365, one specimen, Molokini Island, Hawaiian Islands, 11 m depth, 16 December 1991, Pauline Fiene-Severns. CASIZ 099063, radula removed, Cocos Channel, off Merizo, Guam, 12 m depth, 30 August 1970, C. Carlson and P. Hoff. CASIZ 099065, four specimens, pinnacle, G. Buoy, Kwajelin Atoll, Marshall Islands, 6 m depth, 5 March 1994, S. Johnson. CASIZ 086659, one specimen, Maliko, Maui, crawling on algal turf, 3 m depth, 14 August 1992, P. Fiene-Severns.

ETYMOLOGY. — *Thuridilla carlsoni* is named for my colleague, Clay Carlson, who, together with Patty Jo Hoff, discovered this species.

DISTRIBUTION. — Hawaiian Islands (present study), Enewetak and Kwajelin, Marshall Islands (present study), Guam (Carlson and Hoff, 1978, as *Elysia gracilis*), Western Australia (Wells and Bryce, 1993), Papua New Guinea (present study).

EXTERNAL MORPHOLOGY. — The body color (Fig. 16C) consists of abundant irregular green pigment spots. The parapodia have anastomosing opaque white blotches covering much of the green pigment. The parapodial margin is light yellow. Immediately inside the marginal band is a series of opaque white spots. The head consists of opaque white with green pigment which extends on to the basal third of the rhinophores. The remainder of the rhinophore is covered with opaque white, except for the burnt orange apex. Opaque white pigment is also present at the anterior end of the foot and head. The inside of the parapodia contains a cream marginal line, followed by a band of opaque white and a broader band of black. Most of the internal surface of the parapodia is green with yellow-green longitudinal lines.

PERICARDIUM AND DORSAL VESSELS (Fig. 19A–C): The pericardium gives rise to paired lateral and posterior vessels. The lateral vessels are bifurcate or more highly branched. The posterior vessels have separate junctions with the pericardium. There are 4–5 multifid, bifid or undivided secondary branches. There may be connections between terminal branches of lateral and posterior vessels.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 19D) differs from other described species in being more highly muscularized. It is approximately the same size as the muscular portion of the buccal mass. The radula was examined in three specimens, one from Papua New Guinea, one from Guam and another from the Hawaiian Islands. There are 20–23 teeth with 35–38 fine denticles on either side of the cutting margin. In the Papua New Guinea specimen, there were 8 teeth in the ventral limb, 9 in the dorsal one and 6 teeth in the ascus. In the Hawaiian specimen, the different portions of the radula were not readily discernible. The teeth (Fig. 20) are broad and triangular, 105–115 μm in length. The numerous denticles are coarse and evenly spaced. They continue on to the dorsal surface of the tooth as fine striations. There is a deep triangular depression in the dorsal surface of the basal portion of the tooth in which the cutting portion of the more posterior tooth rests. The posterior end of the tooth is notched.

REPRODUCTIVE SYSTEM (Fig. 19E). — The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the spherical ampulla and the female gland mass. At this point, there is also a junction of the elongate duct of

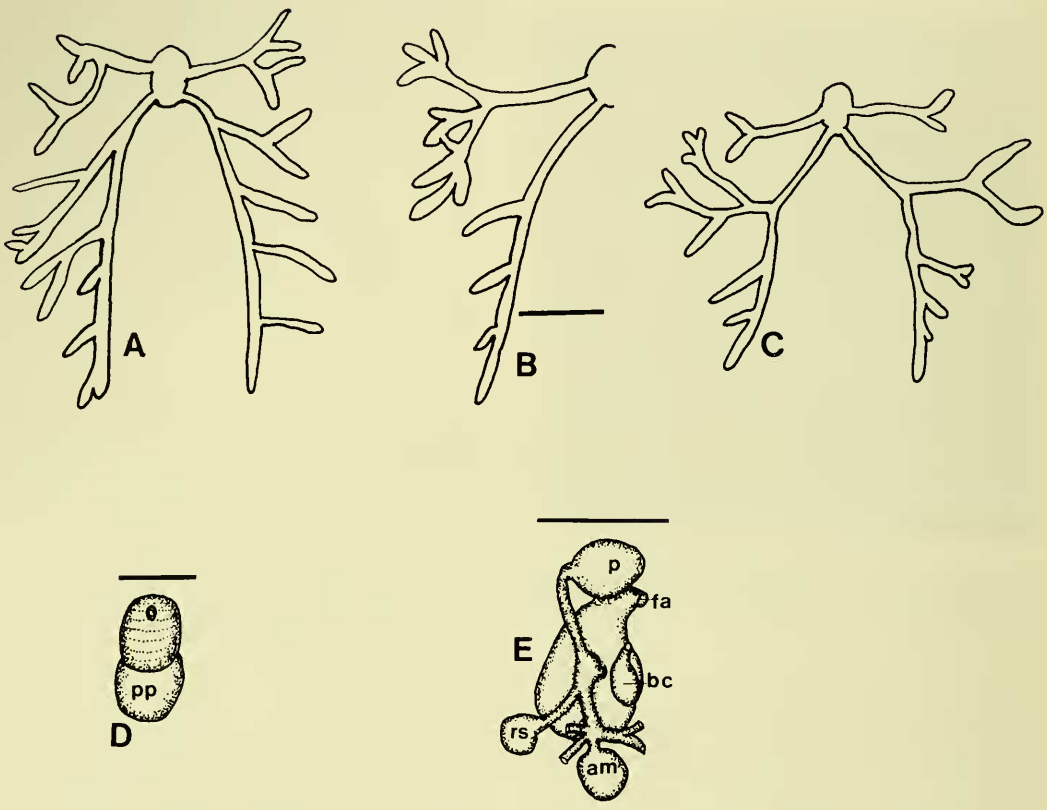

FIGURE 19. *Thuridilla carlsoni* sp. nov. A—C. Branching of pericardial vessels, scale = 5.0 mm. D. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25mm. E. Distal reproductive organs: am = ampulla, bc = bursa copulatrix, fa = female aperture, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

the spherical receptaculum seminis. The small bursa copulatrix empties via a short duct into a separate gonopore. The vas deferens emerges near the junction of the ampulla and associated ducts and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, bulbous penis.

DISCUSSION. — This species was originally recorded from Guam as *Elysia gracilis* Risbec, 1928. However, from the original description of *T. gracilis* it is difficult to determine the identity of the species. The body is greenish with about 8 white longitudinal lines along the side of the parapodia. The edge of the parapodia, the edge of the foot and the anterior portion of the rhinophores are orange. These features suggest that this species may be a pale specimen of *T. bayeri*, but this is inconclusive. Risbec's specimen of *T. gracilis* had approximately ten denticles along either side of the radular tooth, far fewer denticles than any material studied here. Owing to differences in coloration and radular denticulation, the present material is described as a distinct species.

Thuridilla carlsoni differs from all other members of the genus in several regards. It is the least derived member of the genus, having almost all plesiomorphic features. The only derived feature is the numerous denticles along the cutting margin of the radular teeth, which is autapomorphic for the genus. It is most closely related to *T. multimarginata* n. sp., though the two differ in coloration and radular dentition. *Thuridilla carlsoni* has scattered green pigment granules while *T. multimarginata* has uniformly green body color. In

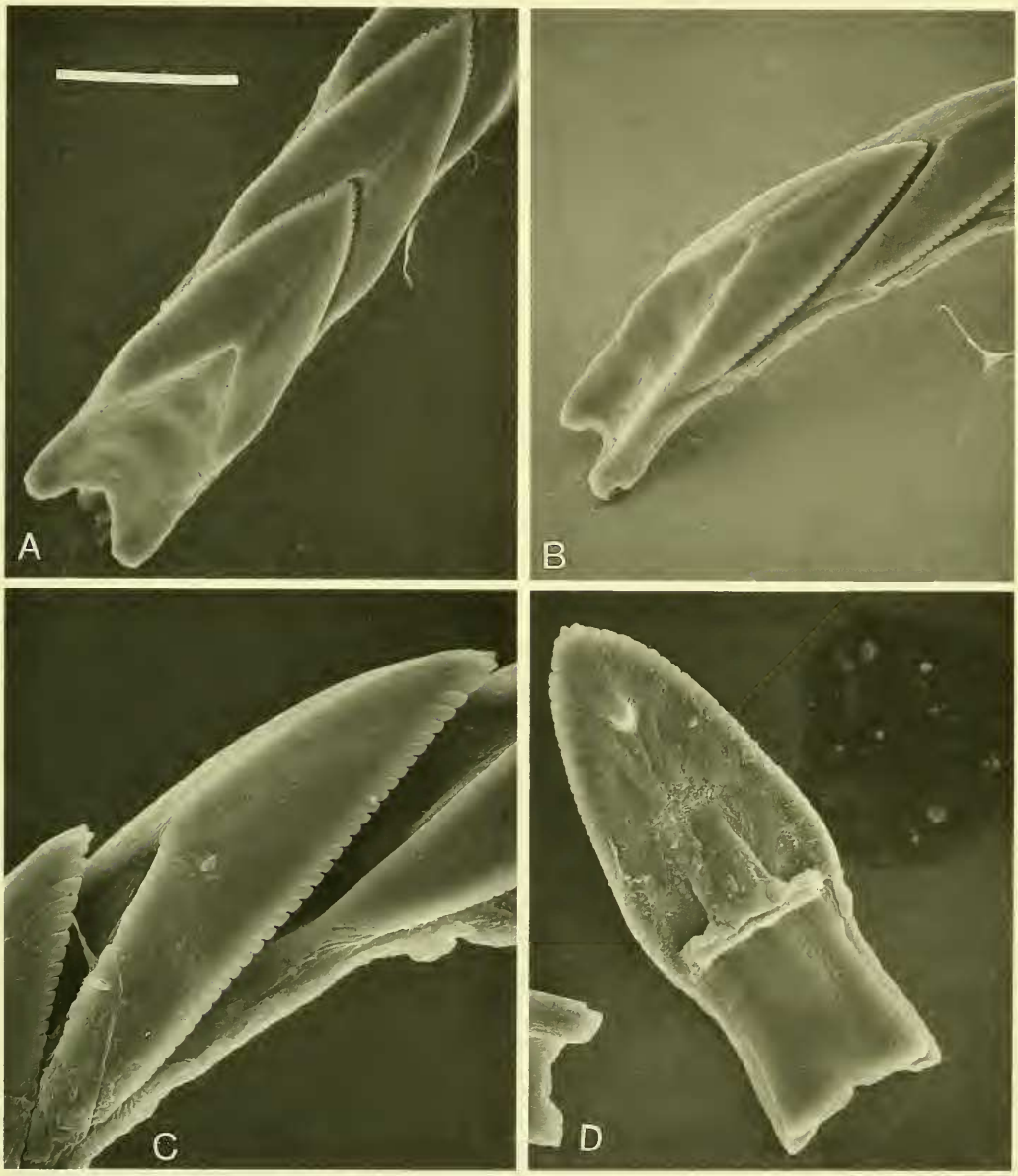

FIGURE 20. *Thuridilla carlsoni* sp. nov. Radular teeth. A. Dorsal view of specimen from Papua New Guinea, CASIZ 065784, scale = 43 μm. B. Lateral view of same specimen, scale= 43 μm. C. Lateral view of specimen from Guam, CASIZ 099063, scale = 20 um. D. Ventral view of same specimen, scale = 25 μm.

T. carlsoni, the parapodial margin is pale cream to yellow while *T. multimarginata* has a series of vividly colored white, orange blue and black bands. The radular teeth of *T. multimarginata* have far fewer denticles than those of *T. carlsoni*. The penis of *T. carlsoni* is bulbous throughout its length, while in *T. multimarginata* it is bulbous basally and narrows in

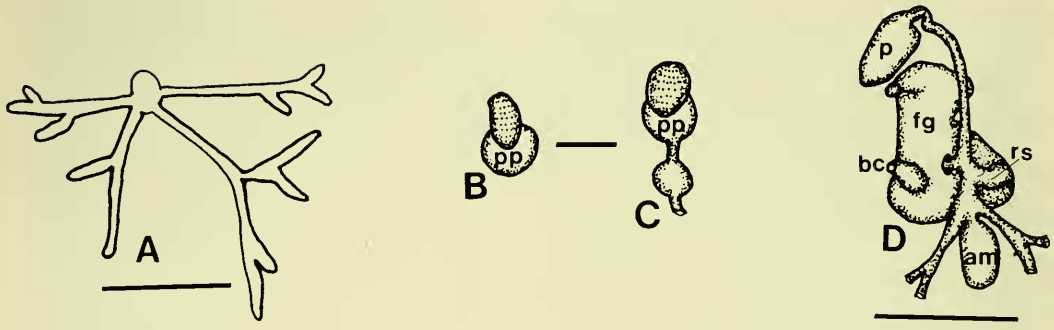

FIGURE 21. *Thuridilla kathae* sp. nov. A. Pericardial branching, scale = 3.0 mm. B. Dorsal view of buccal mass. C. Ventral view of buccal mass. B., C. pp = pharyngeal pouch, scale = 0.25mm. D. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, fg = female gland mass, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

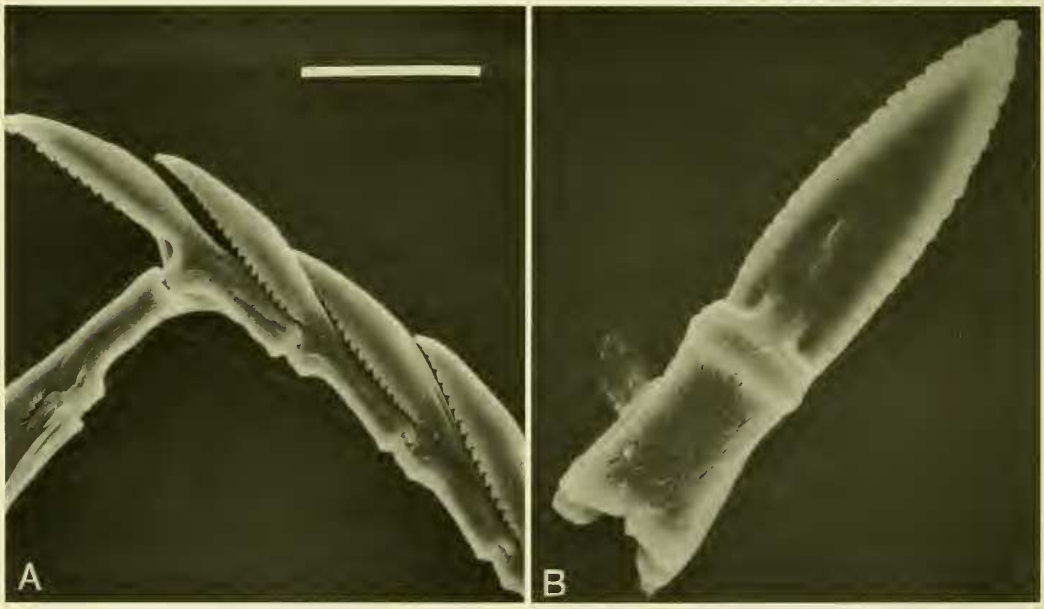

FIGURE 22. *Thuridilla kathae* sp. nov. Radular teeth of specimen from Indonesia, CASIZ 078575. A. Lateral view, scale = 30 μm. B. Ventral view, scale = 15 μm.

the distal half.

The color of *T. carlsoni* is most similar to *T. flavomaculata* n. sp. and *T. kathae* n. sp. All three of these species have green body color and a cream to yellowish parapodial margin. In *T. carlsoni* the green pigment is reticulated with white, while in the other two species the green is solid. Reticulate pigment is also present on

the head, while in *T. flavomaculata* and *T. kathae* opaque white pigment patches are present on the head.

Thuridilla carlsoni has broad radular teeth while both *T. kathae* and *T. flavomaculata* have narrow teeth. The latter two species also have smaller radular teeth and also lack a prominent dorsal notch on the teeth.

9. Thuridilla kathae sp. nov.

TYPE MATERIAL. — Holotype: CASIZ 099064, 5 km wsw of Mora Mora Resort, 20 km n of Tulear, Madagascar, 2 m depth, 7 April 1989, T. M. Gosliner.

Paratypes: CASIZ 070278, two specimens, dissected, Manado, Sulawesi, Indonesia, 3 m depth, 28 May 1989, P. Fiene-Severns. CASIZ 078575, two specimens, one dissected, Bunaken Island, Manado, Sulawesi, Indonesia, 3 m depth, 11 May 1991, P. Fiene-Severns. CASIZ 085890, one specimen, dissected, Cemetery Beach, n. end Maricaban Island, off Luzon, Philippines, 2 m depth, 22 March, 1993, T. M. Gosliner. CASIZ 086705, one specimen, Lebantour, Flores, Indonesia, under rock, 2 m depth, 26 April 1992, P. Fiene-Severns. CASIZ 093951, two specimens, Bunaken Island, Sulawesi, Indonesia, 20 October 1993, P. Fiene-Severns.

ETYMOLOGY. — *Thuridilla kathae* is named for my colleague, Kathe Jensen, who has done much to advance our knowledge of the Sacoglossa and *Thuridilla*, in particular.

DISTRIBUTION. — Philippines, Indonesia and Madagascar (all present study).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 16D) are a rich green with a scattering of large and small opaque white spots. The large spots form low papillae. The margin of the parapodia is cream to light yellow. There is a y-shaped opaque white mark on the head that extends on to the base of the rhinophores. This white is followed by an area of green and then a second patch of opaque white. The tips of the rhinophores are ornamented with orange. Orange pigment is also present on the anterior margin of the foot.

PERICARDIUM AND DORSAL VESSELS (Fig. 21A). — Paired lateral and posterior vessels emerge from the pericardium The lateral branches contain multiple secondary branches. The posterior branches originate separately from the pericardium and have one or two simple or bifid branches.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 21B, C), though larger than the muscular portion of the mass, is relatively smaller than most other species. The radula was examined in a single specimen from Indonesia. There are 24 teeth with 17–18 coarse denticles on either side of the cutting margin. There were 6 teeth in the ventral limb, 6 in the dorsal one and 12 teeth in the ascus. The teeth (Fig. 22) have a relatively short base and elongate triangular portion.

REPRODUCTIVE SYSTEM (Fig. 21D). — The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the ovoid ampulla and the female gland mass. At this point, there is also a junction of the short duct of the spherical receptaculum seminis. The small bursa copulatrix empties via a short duct into a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, bulbous penis.

DISCUSSION. — *Thuridilla kathae* is similar in appearance to *T. carlsoni* and *T. flavomaculata*, and is most closely related to *T. flavomaculata*. The differences between *T. carlsoni* and the other two species are enumerated in the previous discussion. In *T. kathae*, orange pigment is present on the distal portion of the rhinophores while in *T. flavomaculata* the distal portion is white with black longitudinal lines. *Thuridilla kathae* lacks yellow spots over the surface of the body that are present in *T. flavomaculata*. In addition to these consistent differences in coloration, *T. kathae* has less highly branched lateral pericardial vessels than does *T. flavomaculata*, but has somewhat more vesicular branching of the posterior vessels. The penial papilla of *T. kathae* is more bulbous than that of *T. flavomaculata*. Other than these relatively minor, but consistent, differences, the two species are similar in most other aspects of their anatomy and appear to be closely related.

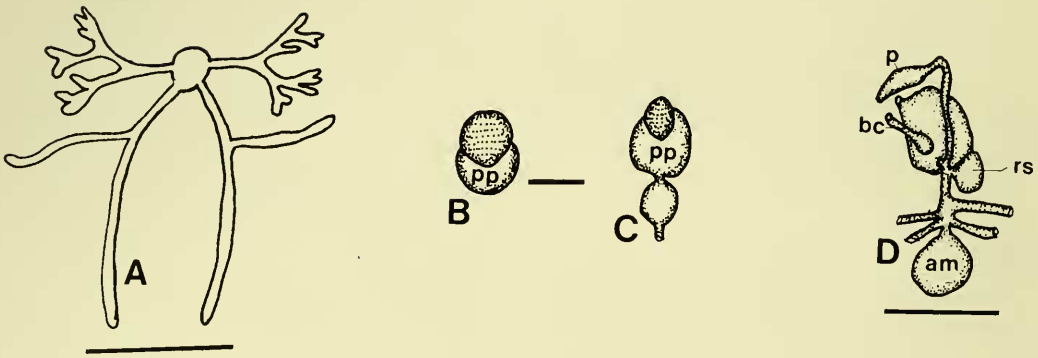

FIGURE 23. *Thuridilla flavomaculata* sp. nov. A. Branching of pericardial vessels, scale = 5.0 mm. B. Dorsal view of buccal mass. C. Ventral view of buccal mass. B., C. pp = pharyngeal pouch, scale = 0.25mm. D. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

10. Thuridilla flavomaculata sp. nov.

TYPE MATERIAL. — Holotype: CASIZ 103557, The Head, Hamilo Bay, Luzon, Philippines, 9 m depth, 4 March 1995, Mel Segarra.

Paratypes: CASIZ 087367, Nain Island, Manado, Sulawesi, Indonesia, under rock, 1.5 m depth, 7 May 1990, P. Fiene-Severns. CASIZ 070278, one specimen, radula removed, Manado, Sulawesi, Indonesia, 3 m depth, 28 May 1989, P. Fiene-Severns. CASIZ 078583, one specimen, dissected, Bunaken Island, Manado, Sulawesi, Indonesia, 3 m depth, 13 May 1991, P. Fiene-Severns. CASIZ 099066, one specimen, radula removed, channel between Cocos Island and Merizo, Guam, 8 m depth, 27 September 1970, C. Carlson and P. Hoff.

ETYMOLOGY. — The epithet *flavomaculata* refers to the yellow spots that ornament the parapodia. This is the only species of *Thuridilla* with many scattered yellow spots.

DISTRIBUTION. — This species is known from Enewetak and Kwajelin, Marshall Islands (Scott Johnson pers. comm.), Indonesia, Luzon, Philippine Islands and Guam (present study).

EXTERNAL MORPHOLOGY. — The animal is green (Fig. 16E) with scattered opaque white and yellow spots. The edge of the parapodia is cream colored. The base of the rhinophores is opaque white with several longitudinal black lines extending along the outer third of the rhinophores.

PERICARDIUM AND DORSAL VESSELS. — Paired lateral and posterior vessels emerge from the pericardium (Fig. 23A). The lateral branches contain multiple secondary branches. The posterior branches originate separately from the pericardium and each have a single undivided branch.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 23B, C), is larger than the muscular portion of the mass, but is somewhat smaller than in other species. The esophageal pouch is muscular, smaller than the buccal mass. The radulae of two paratypes were examined, but the radula of one was lost during preparation. The precise number of teeth could not be determined, since the ascus and portions of the ventral limb of the radula were lost. There are 7 teeth forming the dorsal limb. Each triangular tooth (Fig. 24) has 18–21 coarse denticles along either side of the cutting margin. The cutting portion is slightly longer than the basal articulating surface.

REPRODUCTIVE SYSTEM (Fig. 23D). — The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the ovoid ampulla and join the female gland mass. At this point, there is also a junction of the short, spherical receptaculum seminis. The small bursa copulatrix exits via an elongate duct, into a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts,

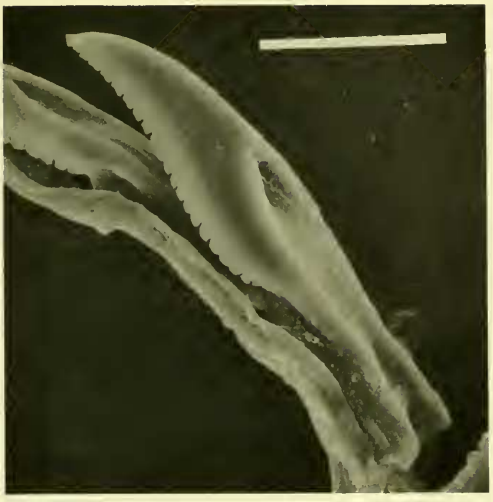

FIGURE 24. *Thuridilla flavomaculata* sp. nov. Radular teeth of specimen from Indonesia, CASIZ 070278, scale= 20 μm.

female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, thin penis.

DISCUSSION. — The differences between this species, *T. carlsoni* and *T. kathae* are discussed in the sections dealing with those species. *Thuridilla flavomaculata* is readily distinguishable from other congeners by its green body color with scattered yellow spots and white apices of the rhinophores with black longitudinal lines.

11. Thuridilla hoffae sp. nov.

Elysia livida Carlson and Hoff, 1978, in part.
Elysia livida Johnson and Boucher, 1983, not Baba, 1955.

TYPE MATERIAL. — Holotype: CASIZ 065773, one specimen, the Quarry, 1 km s of Cape Croiselles, Madang Province, Papua New Guinea, 11 February 1988, T. M. Gosliner.

Paratypes: CASIZ 071248, one specimen, Planet Rock, 10 km s. of Madang, Papua New Guinea, 5 m depth, 16 February 1988, G. Williamson. CASIZ 071242, two specimens, one dissected, Barracuda Point, e side Pig Island, Madang Harbor, Madang, Papua New Guinea, 10 m depth, 8 February 1988, J. Mizeu. CASIZ 069936, one specimen, Horseshoe Cliffs, 1 km wnw of Onna Village, Okinawa, Ryukyu Islands, 10 m depth, 18 April 1987, R. F. Bolland. CASIZ 071241, one specimen, dissected, Madang Lighthouse, Papua New Guinea, 10 m depth, 15 January 1988, R. C. Willan. CASIZ 065361, one specimen, Barracuda Point, e side Pig Island, Madang Lagoon, Papua New Guinea, 15 m depth, 17 January 1988, R. C. Willan. CASIZ 071243, two specimens, se side Pig Island, Madang Lagoon, Papua New Guinea, 16 m depth, 24 January 1988, T. M. Gosliner. CASIZ 086486, one specimen, dissected, barrier reef between Pig Island and Rasch Passage, Madang Lagoon, Papua New Guinea, 8 June 1992, T. M. Gosliner. CASIZ 071247, Barracuda Point, e. side Pig Island, Madang Lagoon, Papua New Guinea, 8 m depth, 14 February 1988, R. C. Willan. CASIZ 073031, one specimen, Rasch Passage, Madang Lagoon, 25 October 1986, G. Williamson. CASIZ 089033, one specimen, Seragaki Beach, 1.3 km ene of Maeki-zaki, Okinawa, Ryukyu Islands, 2 m depth, 3 April 1993, R. F. Bolland. CASIZ 071248, one specimen, Planet Rock, Madang, Papua New Guinea, 12 m depth, 16 February 1988, G. Williamson.

ETYMOLOGY. — *Thuridilla hoffae* is named for my colleague Patty Jo Hoff who, together with Clay Carlson, first discovered this species.

DISTRIBUTION. — Enewetak, Marshall Islands (Johnson and Boucher, 1983, as *Elysia livida*, S. Johnson, pers. comm.), Guam (Carlson and Hoff, 1978, as *E. livida*, in part), Okinawa (present study), Papua New Guinea (present study).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 16F) are black. The margin of the parapodia contains a vivid orange line of reflective granules. Below the margin, bright, reflective blue-green blotches cover most of the parapodia. The head is black with blue-green pigment covering most of the rhinophores. The anterior margin of the foot has an orange line.

PERICARDIUM AND DORSAL VESSELS. — Only posterior vessels were present in the three specimens examined (Fig. 25A–C). These have a common junction with the pericardium. Each posterior vessel has 2–3 secondary vessels with multifid, bifid or undivided branches.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 25D) is much larger than the muscular portion of the buccal mass. The radular teeth (Fig. 26) are triangular with 16–19 coarse denticles along either side of the cutting margin and continue on the dorsal tooth surface

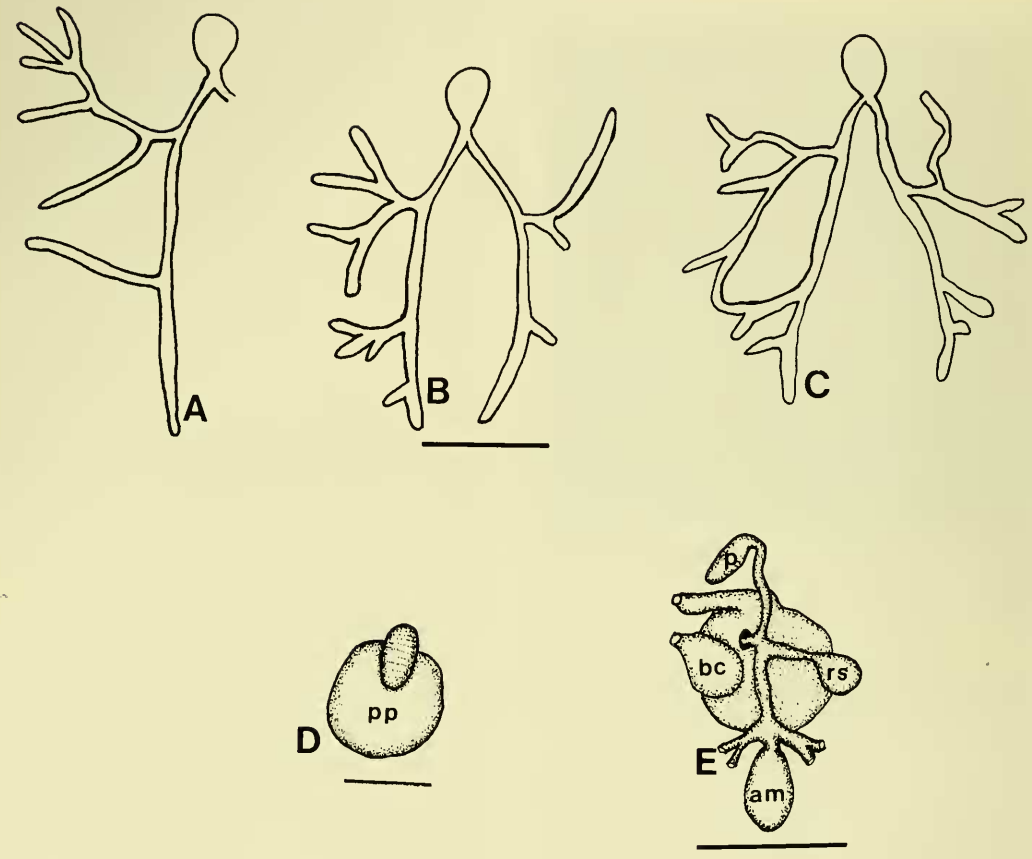

FIGURE 25. *Thuridilla hoffae* sp. nov. A.-C. Branching of pericardial vessels, scale = 5.0 mm. D. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25mm. E. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

as striations.

REPRODUCTIVE SYSTEM (Fig. 25E). The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the ovoid ampulla and together join the female gland mass. At this point, there is also a junction of the elongate duct of the spherical receptaculum seminis. The pyriform bursa copulatrix exits via a short duct at a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis, by means of an elongate duct. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, thin penis.

DISCUSSION. — This species is most similar in color to *T. livida* and is most closely related to this species. The important morphological distinctions between *T. hoffae* and *T. livida* were described previously in the discussion of *T. livida*.

12. Thuridilla albopustulosa sp. nov.

Elysia sp. 2 Gosliner, 1987: 54, fig. 47

TYPE MATERIAL. — Holotype: CASIZ 099068, one specimen, Cement Mixer Reef, Madang Lagoon, Papua New Guinea, 11 January 1988, R. C. Willan.

Paratypes: SAM A 35269, one specimen, dis-

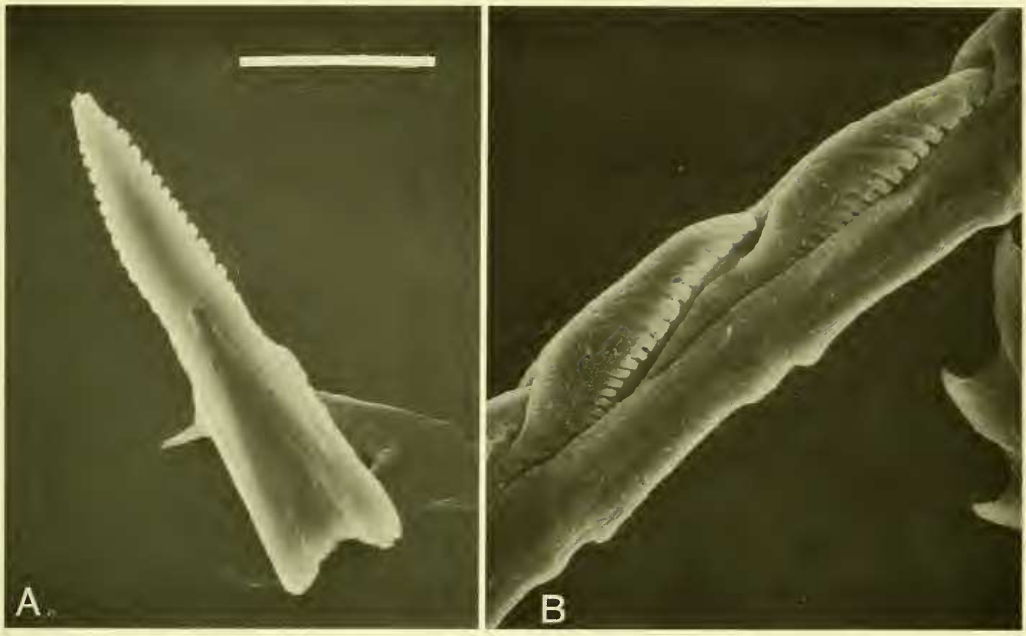

FIGURE 26. *Thuridilla hoffae* sp. nov. Radular teeth of specimens from Papua New Guinea. A. Dorsal view, CASIZ 086486, scale = 15 μm. B. Lateral view, CASIZ 071241, scale = 20 μm.

sected, Mbibi, Sodwana Bay National Park, Natal, South Africa, 6 May 1982, T. M. Gosliner. CASIZ 078564, one specimen, Bunaken Island, Manado, Sulawesi, Indonesia, 5 m depth, 20 May 1991, P. Fiene-Severns. CASIZ 074208, one specimen, Passe du Bois, Aldabra Atoll, Seychelles, 22 March 1986, T. M. Gosliner. CASIZ 099067, one specimen, Madang Resort, Papua New Guinea, 1 February 1988, R. C. Willan. CASIZ 085882, two specimens, one dissected, 3 km e of Lighthouse, near Dakak Resort, Mindinao, Philippines, 3 m depth, 1 April 1993, T. M. Gosliner. CASIZ 087034, one specimen, Bunaken Island, Manado, Sulawesi, Indonesia, under rock, 3 m depth, 20 May 1990, P. Fiene-Severns.

ETYMOLOGY. — The name *albopustulosa* is derived from the white pustules present on the parapodia.

DISTRIBUTION. — Philippines, Papua New Guinea, Indonesia, Aldabra Atoll (all present study), South Africa (Gosliner, 1987).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 29B) are light blue with scattered black pigment especially near the foot at the base of the parapodia. The parapodial margin is opaque white. The parapodia are covered with scattered opaque white or cream spots or longitudinal bands. The head has diffuse black pigment along its margins. The basal third of the rhinophores is opaque white. The outer two-thirds is bright red with a scattered patch or two of opaque white in the middle of the red. The red pigment extends farther basally on the outer side of the rhinophore than on the inner side. This creates the appearance of a diagonal rather than transverse band. The anterior margin of the foot is blue.

PERICARDIUM AND DORSAL VESSELS. — The arrangement of the vessels was examined in four specimens (Fig. 27A–D). Both lateral and posterior vessels are present. The lateral vessels are undivided, bifurcate or trifurcate. The posterior vessels have a common origin from the posterior end of the pericardium. The anterior duct of the posterior vessel usually joins with the the lateral vessels.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 27E), is much larger than the

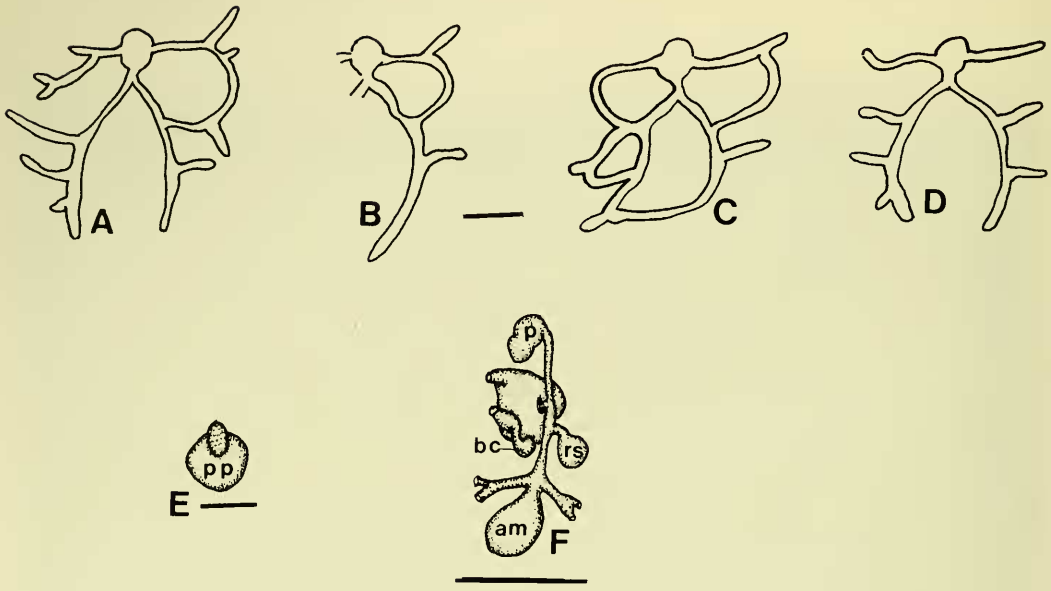

FIGURE 27. *Thuridilla albopustulosa* sp. nov. A.–D. Branching of pericardial vessels, scale = 3.0 mm. E. Dorsal view of buccal mass, pp = pharyngeal pouch, scale = 0.25 mm. F. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

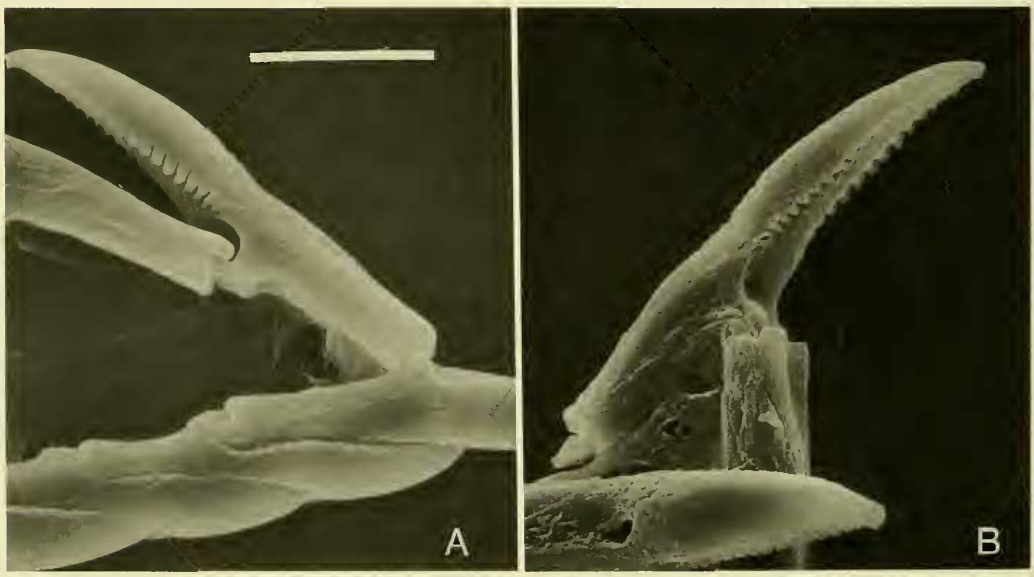

FIGURE 28. *Thuridilla albopustulosa* sp. nov. Radular teeth. A. Lateral view of specimen from South Africa, SAM A35269, scale = 10 μm. B. Lateral view of specimen from Philippines, CASIZ 085882, scale = 10 μm.

muscular portion of the mass. The radula consists of 16 teeth in one specimen from the Philippines and 21 teeth in a specimen from South Africa. There are 11–12 teeth in the ventral branch of the radula and 5–9 in the dorsal one. No discarded teeth were found in the ascus of either specimen examined. The individual teeth (Fig. 28) are triangular with 13–16 coarse denticles along the cutting margin. The cutting portion is slightly longer than the base of the tooth.

REPRODUCTIVE SYSTEM (Fig. 27F). — The ovotestis, prostate and albumen glands are diffuse and are arranged as in *T. bayeri*. Their ducts join the ovoid ampulla and the female gland mass. At this point, there is also a junction of the short duct of the spherical receptaculum seminis. The curved bursa copulatrix empties via an elongate duct at a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, bulbous penis.

DISCUSSION. — The similarity of *T. vatae* with *T. albopustulosa* is included in the discussion of the former species. The lighter bluish body color of *T. albospustulosa* with diagonal rather than transverse red pigment on the rhinophores clearly distinguishes it externally from *T. vatae*. It is also more distantly related to *T. virgata* and *T. moebii*, all of which share the derived feature of an enlarged pharyngeal pouch.

13. Thuridilla undula sp. nov.

Thuridilla sp. Yonow, 1994: 106, figs. 5B, 6B.

TYPE MATERIAL. — Holotype: CASIZ 099072, one specimen, Cement Mixer Reef, Madang Lagoon, 3 m depth, 21 August 1989, M. T. Ghiselin.

Paratypes: CASIZ 099071, one specimen, Rasch Passage, Madang Lagoon, Papua New Guinea, 10 m depth, 20 August 1989, M. T. Ghiselin. CASIZ 099070, one specimen, dissected, Hole in the Wall, n. of Cape Croiselles, Madang Province, Papua New Guinea, 1 m depth, 22 July 1989, T. M. Gosliner. CASIZ 099069, one specimen, buoy 7, Palau, 1 m depth, 21 July 1977, C. Carlson and P. Hoff. CASIZ 103558, one specimen, n. side of n.w. passage, Puerto Galera, Mindoro, Philippine Islands, 10 m depth, 28 February 1995, M. Miller.

ETYMOLOGY. — This species is named for the undulating bands along and below the parapodial margins.

DISTRIBUTION. — This species is known from Papua New Guinea, Guam, Palau and the Philippines (present study) and the Maldives (Yonow, 1994).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 29A) are turquoise bluish green. The parapodial margin is a broad undulating band of burnt orange. Below that is a narrow undulating line of black. This is followed by an undulating region of vivid blue reflective pigment. There is black and reflective blue pigment on the head. The base of the rhinophores are the same color as the rest of the body. At about the middle of the rhinophores are narrow bands of blue and black. The apex has a broad orange band. Orange, black and blue bands are also present on the anterior margins of the foot.

PERICARDIUM AND DORSAL VESSELS. — There is considerable variation in the extent of branching of the vessels in the two specimens examined (Fig. 30A, B), but the basic pattern is similar. In both cases, lateral and posterior vessels are present. The lateral vessels are trifurcate or more highly branched. The posterior vessels have an elongate common origin from the pericardium. The posterior vessels may be undivided or may have 2–3 undivided or bifurcate branches.

BUCCAL MASS AND RADULA. The pharyngeal pouch (Fig. 30C, D) is larger than the more muscular portion of the buccal mass, although it is relatively smaller than that of some other species. The esophageal pouch is ovoid and more elongate than in other species. The radula was examined in a single specimen from Papua New Guinea. There are 28 teeth with 16–18 coarse denticles on either side of the cutting margin. There were 11 teeth in the ventral limb, 9 in the dorsal one and 8 teeth in the ascus. The base of the teeth (Fig. 31) is shorter than the elongate triangular portion.

REPRODUCTIVE SYSTEM (Fig. 30E). — The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the spherical ampulla and join the female gland mass. At this point, there is also a junction of the elongate

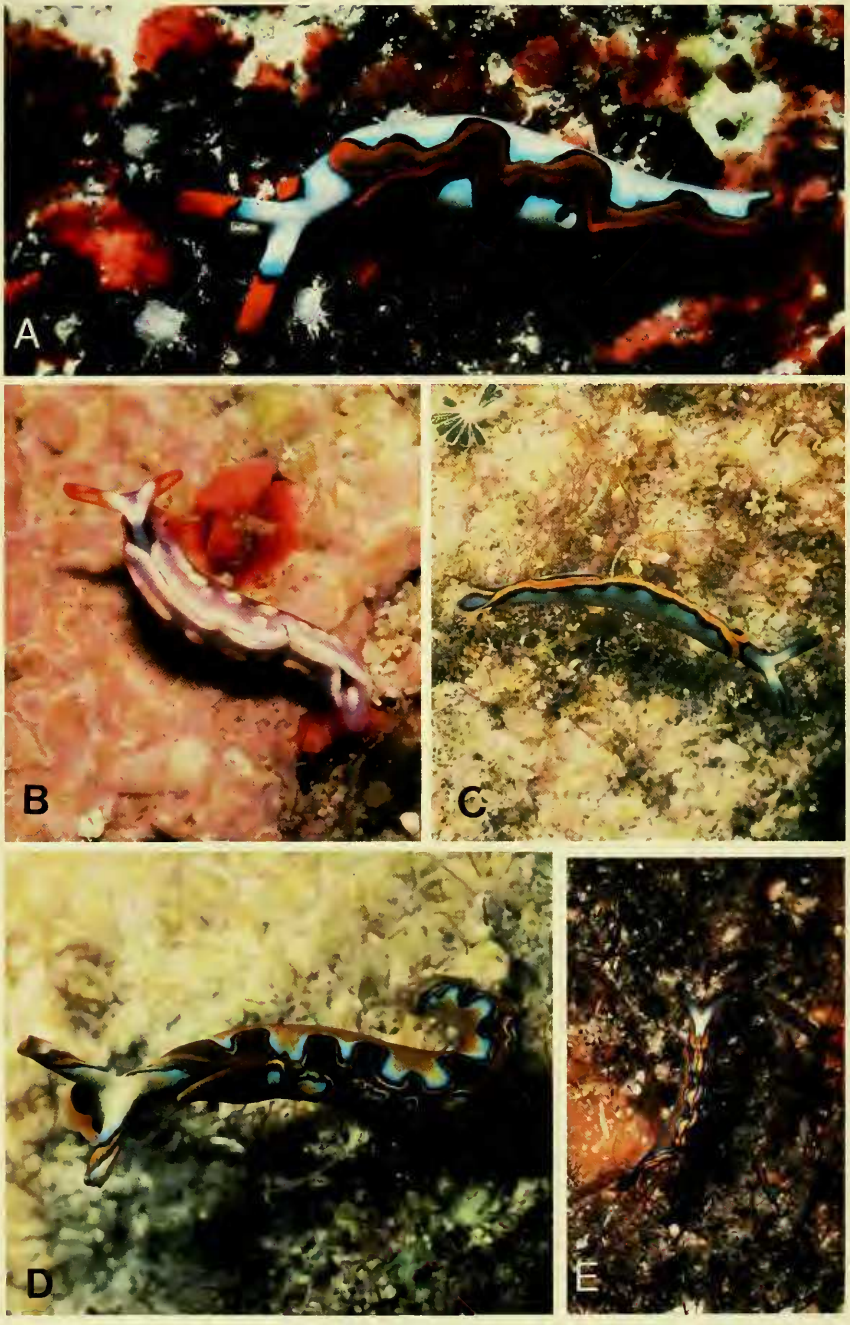

FIGURE 29. Living animals. A. *Thuridilla undula* sp. nov., Madang, Papua New Guinea, 25 mm in length. B. *Thuridilla albopustulosa* sp. nov., Madang, Papua New Guinea, 15 mm in length. C. *Thuridilla indopacifica* sp. nov., Sodwana Bay, South Africa, 18 mm in length. D. *Thuridilla neona* sp. nov., Midway Atoll, 22 mm in length. E. *Thuridilla multimarginata* sp. nov., Sodwana Bay, South Africa, 9 mm in length.

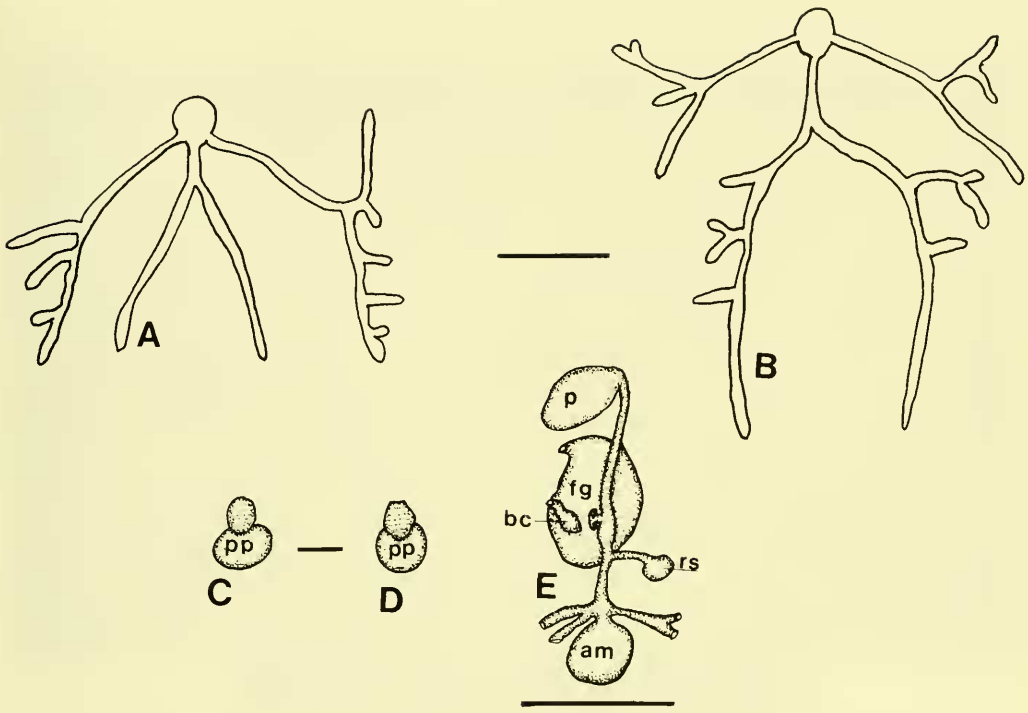

FIGURE 30. *Thuridilla undula* sp. nov. A., B. Branching of pericardial vessels, scale = 5.0 mm. C. Dorsal view of buccal mass. D. Ventral view of buccal mass. C., D. pp = pharyngeal pouch, scale = 0.20 mm. E. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, fg = female gland mass, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

duct of the spherical receptaculum seminis. The small bursa copulatrix empties via a moderately long duct at a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the large, unarmed, bulbous penis.

DISCUSSION.—*Thuridilla undula* is a strikingly beautiful member of the genus. It is similar in coloration to *T. neona* sp. nov. Both species have a turquoise body with burnt orange, black and blue undulating parapodial bands. Despite these similarities in color, there are some consistent differences between the species. In *T. neona*, there are additional bright orange markings present on the parapodia, anterior margin of the foot and rhinophores. In *T. undula* the orange, blue and black markings on the rhinophores are transverse bands, while in *T. neona* they are diagonal.

The two species differ markedly in other aspects of their morphology. In *T. undula*, both lateral and posterior vessels emerge from the pericardium, while in *T. neona* only posterior vessels are present. The radular teeth of *T. undula* are narrower and have a deeper dorsal notch than do those of *T. neona*. Also, the denticles of *T. undula* do not continue as striations on the lateral and dorsal surfaces of the the teeth as they do in *T. neona*. In *T. undula*, the denticles extend below the level of the tooth margin, while in *T. neona* the denticles are flush with the margin.

Thuridilla undula appears to be most closely related to *T. lineolata*. The two have similar coloration and differ from other members of their clade by lacking an expanded pharyngeal

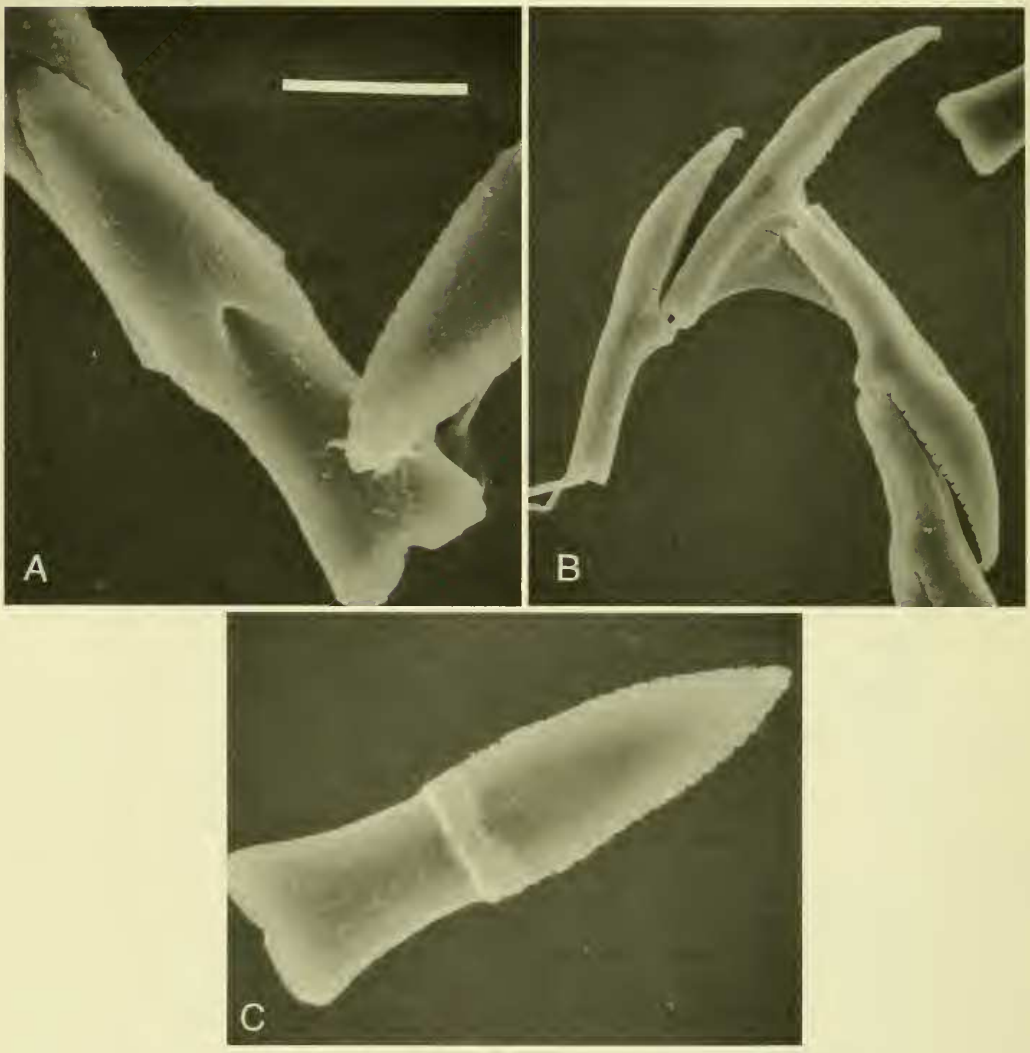

FIGURE 31. *Thuridilla undula* sp. nov. Radular teeth of specimen from Papua New Guinea, CASIZ 099070. A. Dorsal view. scale = 10 μm. B. Lateral view, scale = 20 μm. C. Ventral view, scale = 10 μm.

pouch or longitudinal white lines on the parapodia. In *T. undula* the lateral branches of the pericardium are highly ramified, while in *T. lineolata* they are only bifurcate. In *T. undula* the posterior vessels have a common junction prior to entering the pericardium while in *T. lineolata* they have separate insertions into the pericardium.

14. Thuridilla neona sp. nov.

TYPE MATERIAL. Holotype: CASIZ 074461, onespecimen, Lanai, Hawaiian Islands, July 1990, S. McLellan.

Paratypes: CASIZ 088551, one specimen, dissected, near white cross n. of harbor entrance, Sand Island, Midway Atoll, 5 June 1993, T. M. Gosliner. CASIZ 076462, three specimens, Hekili Point, Maui, Hawaiian Islands, on algal turf, 0.5 m depth, October

1990, C. Pittman.

ETYMOLOGY. — This species is named for the bright "electric" colors which adorn the parapodia, head and anterior margins of the foot.

DISTRIBUTION. — Windward and leeward Hawaiian Islands (present study; Scott Johnson, pers. comm.).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 29D) are green with a slight bluish tinge. The margin of the parapodia is lined with a broad, undulating band of burnt orange. Inside of that are thin undulating bands of reflective bright orange, black and reflective bright blue. The head and base of the rhinophores are opaque white. The head has a series of lines. The lateral margin of the head has lines of reflective blue followed by black, reflective orange, and burnt orange. The rhinophores have a series of diagonal lines of reflective blue, black, reflective orange, burnt orange and white pigment. The apex of the rhinophores is orange. The anterior margin of the foot is burnt orange.

PERICARDIUM AND DORSAL VESSELS (Fig. 32A, B). — Lateral vessels are absent. The posterior vessels have separate origins from the pericardium. The specimen from Lanai had a single, undivided branch emerging from the middle of either vessel. The specimen from Midway has an asymmetrical and complex branching pattern with connections between adjacent branches.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 32C) is larger than the muscular portion, though not as large relatively as many other species. The radula was examined in one specimen from Midway Island and consists of 23 teeth. Eight teeth are present in the ascus, 6 in the ventral limb and 9 in the dorsal one. The teeth (Fig. 33) are triangular with 22–24 coarse denticles that continue dorsally as prominent striations. The denticles are unusual in that they do not extend below the level of the tooth margin. This is not owing to wear as this feature is present in newly formed teeth as well as older ones.

REPRODUCTIVE SYSTEM (Fig. 32D). — The ovotestis, prostate and albumen glands are diffuse and are arranged as in *T. bayeri*. Their ducts join the massive spherical ampulla and the female gland mass. At this point, there is also a junction of the elongate duct of the spherical receptaculum seminis. The moderately large bursa copulatrix empties via a short duct into a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, club-shaped penis.

DISCUSSION. — *Thuridilla neona* resembles *T. undula* in its coloration. The similarities and differences between these taxa are compared in the discussion of *T. undula*.

Thuridilla neona appears to be most closely related to *T. hopei* (Verany, 1853) from the Mediterranean. The two species differ markedly in their coloration (present study). *Thuridilla hopei* has a bluish body color, but lacks the burnt orange, black and blue lines around the parapodial margin that are present in *T. neona*.

Internally, *T. neona* appears to have wider teeth than *T. hopei*. The penial bulb in *T. neona* is widest distally, while that of *T. hopei* is widest proximally.

15. Thuridilla indopacifica sp. nov.

Elysia sp. 1 Gosliner, 1987: 54, fig. 46.
Thuridilla sp. Wells and Bryce, 1993: 67, fig. 73.

TYPE MATERIAL. — Holotype: CASIZ 099073, one specimen, Middle Camp, Aldabra Atoll, 2 m depth, 18 March 1986, T. M. Gosliner.

Paratypes: SAM A 35270, one specimen, Mbibi, Sodwana Bay National Park, Natal, South Africa, 1 m depth, 6 May 1981, T. M. Gosliner. SAM A 35294, five specimens, Mbibi, Sodwana Bay National Park, Natal, South Africa, 6 May 1981, T. M. Gosliner. SAM A 35279, two specimens, one dissected, Mbibi, Sodwana Bay National Park, Natal, South Africa, 2 m depth, 6 May 1981, T. M. Gosliner. SAM A 35277, one specimen, Mbibi, Sodwana Bay National Park, Natal, South Africa, T. M. Gosliner. CASIZ 073974, five specimens, Mbibi, Sodwana Bay National Park, Natal, South Africa, 6 May 1981, T. M. Gosliner. CASIZ 073972, one specimen, Mbibi, Sodwana Bay National Park, Natal, South Africa, May 1982, T. M. Gosliner. CASIZ 074240, two specimens, one dissected, Middle Camp, Aldabra Atoll, Seychelles, 18 March 1986, T. M. Gosliner.

ETYMOLOGY. — This species is named for

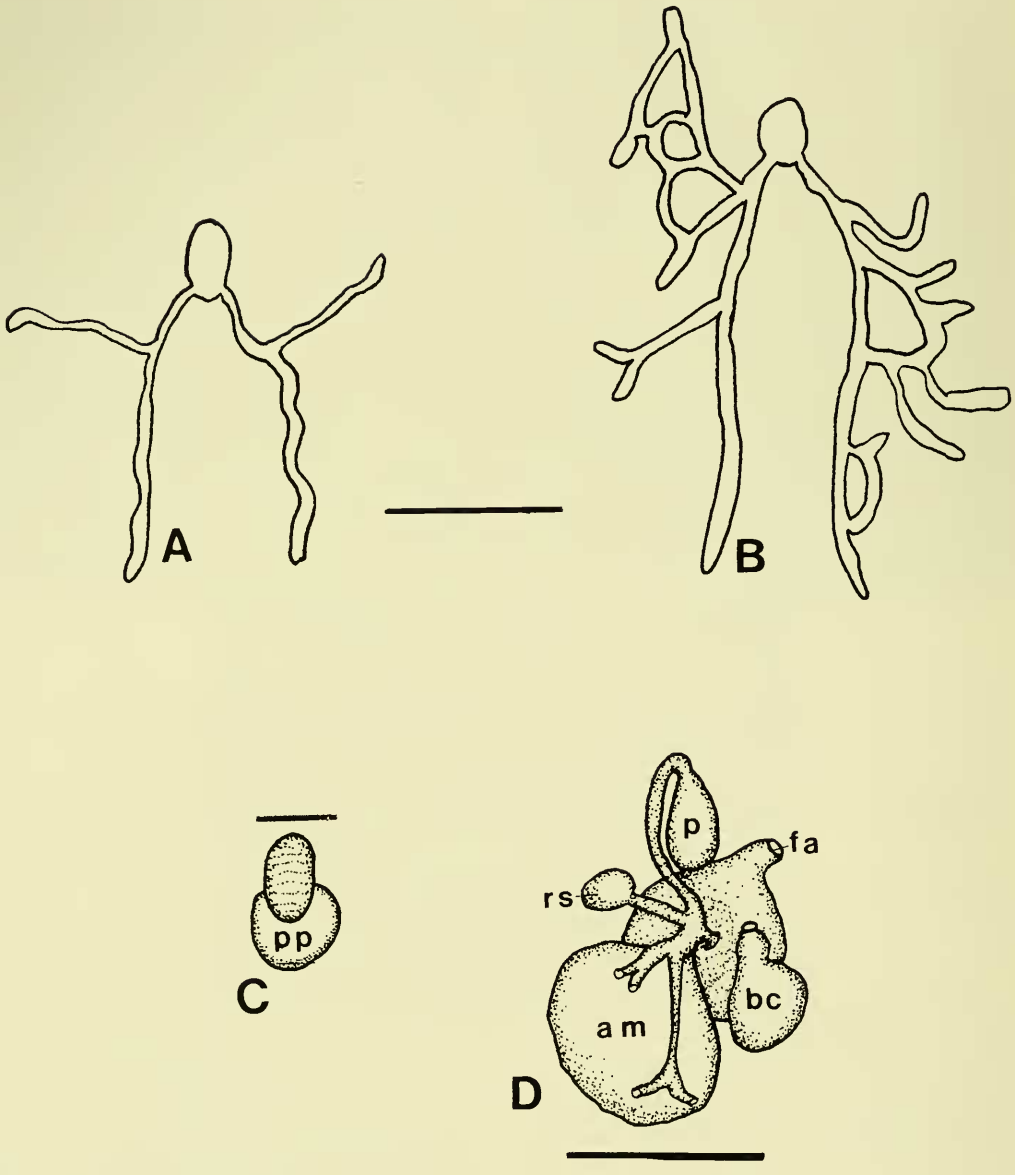

FIGURE 32. *Thuridilla neona* sp. nov. A., B. Branching of pericardial vessels, scale= 5.0 mm. C. Dorsal view of buccal mass, pp= pharyngeal pouch, scale = 0.25 mm. D. Distal reproductive organs: am = ampulla, bc = bursa copulatrix, fa = female aperture, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

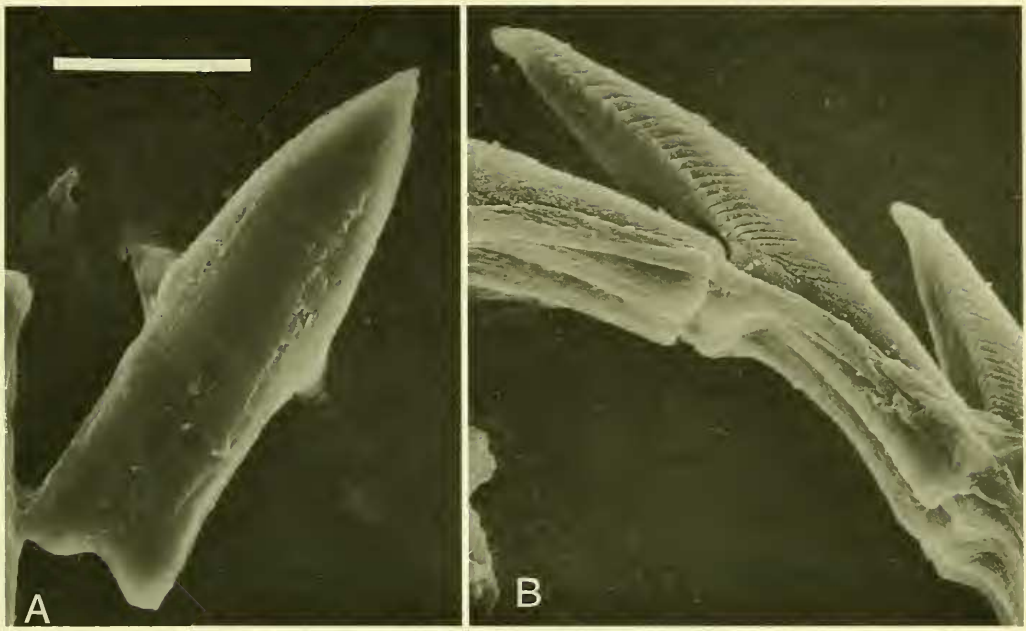

FIGURE 33. *Thuridilla neona* sp. nov. Radular teeth of specimen from Midway Atoll, CASIZ 088551. A. Dorsal view, scale = 15 μm. B. Lateral view, scale = 15 μm.

the Indo-Pacific tropics, the region where *Thuridilla* reaches its highest diversity.

DISTRIBUTION. — South Africa (Gosliner, 1987), Aldabra Atoll (present study), Western Australia (Wells and Bryce, 1993).

EXTERNAL MORPHOLOGY. — The body is green (Fig. 29C), covered with minute opaque white spots. The parapodia are lined with a thin band of black, followed by a broad band of orange, an irregular band of black with a series of ventral extensions of pigment. Between the black extensions are patches of reflective bright blue. The head is covered with opaque white, which extends on to the basal half of the rhinophores. Above this is a diffuse band of blue followed by black, orange and blue bands. The anterior margin of the foot has black, orange, black and blue bands.

PERICARDIUM AND DORSAL VESSELS. — Lateral vessels are absent (Fig. 34A, B). The posterior vessels have separate origins from the pericardium. Two to five undivided or bifurcate vessels emerge from each lateral vessel.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 34C, D), is much larger than the muscular portion of the mass. The radula, examined in a single specimen from South Africa, contains 29 teeth. There are 12 teeth in the ascus, 10 in the ventral limb and 7 in the dorsal one. The teeth (Fig. 35) are triangular with 17–19 coarse denticles that continue as prominent striations on to the dorsal surface of the teeth. The basal portion of the teeth is slightly shorter than the cutting margin.

REPRODUCTIVE SYSTEM (Fig. 34E). — The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the ovoid ampulla and together join the female gland mass. At this point, there is also a junction of the short duct of the spherical receptaculum seminis. The large bursa copulatrix empties via a short duct at a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, club-shaped penis.

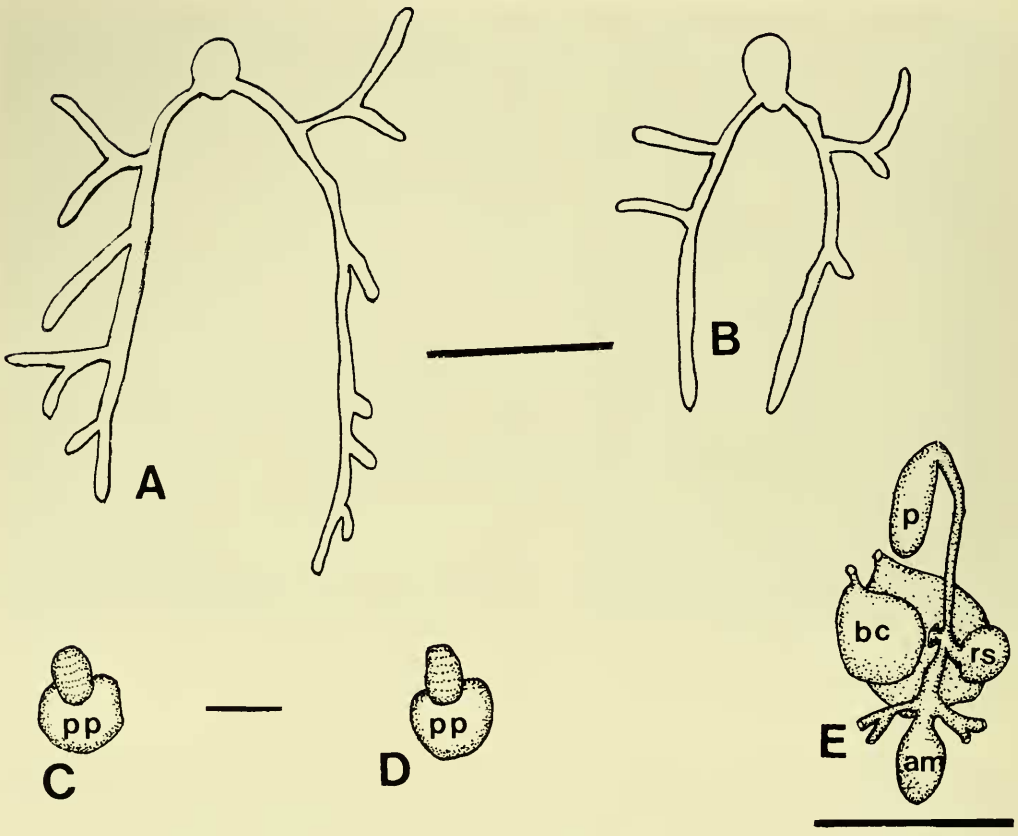

FIGURE 34. *Thuridilla indopacifica* sp. nov. A., B. Branching of pericardial vessels, scale = 5.0 mm. C. Dorsal view of buccal mass, pp = pharyngeal pouch, scale = 0.25 mm. D. Ventral view of buccal mass, pp= pharyngeal pouch, scale = 0.25 mm. E. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

DISCUSSION. — *Thuridilla indopacifica* appears to be most closely related to *T. picta* (Verrill, 1901), which is known from the tropical Atlantic (Marcus and Marcus, 1967, as *E. duis*; Ortea, Luque and Templado, 1988). Both species have a greenish body color with orange and blue marking on the parapodia. *Thuridilla indopacifica* also has a black parapodial line that is sometimes absent in *T. picta*. The parapodial lines of *T. picta* are far more undulating than in *T. indopacifica*. *T. indopacifica* also has more white pigment on the head than does *T. picta*.

The branching of the pericardial vessels is similar in the two species. Both lack lateral vessels and have only paired posterior vessels with separate insertions into the pericardium. In *T. indopacifica*, the radular teeth have denticles that extend well below the margin of the tooth, while in *T. picta* they are flush with the margin. The penis of *T. indopacifica* is club- shaped, while it is far more bulbous in *T. picta*.

16. Thuridilla multimarginata sp. nov.

Elysia sp. 3 Gosliner, 1987: 55, fig. 48.

TYPE MATERIAL. — Holotype: CASIZ 088426, patch reef inside lagoon, n of Sand Island, Midway Atoll, 3 m depth, 1 June 1993, Pauline Fiene-Severns.

Paratypes: SAM A35282, one specimen, radula re-

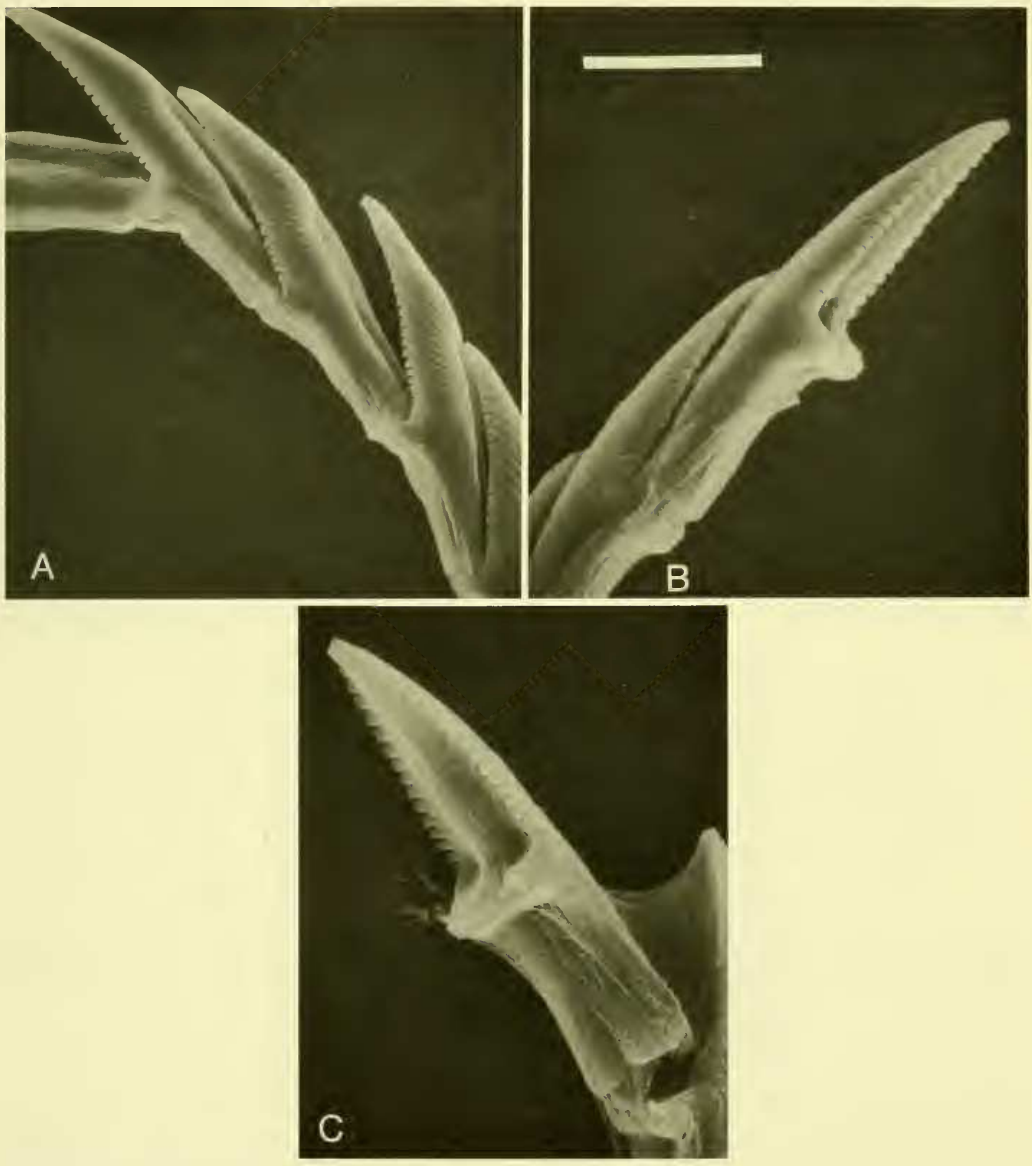

FIGURE 35. *Thuridilla indopacifica* sp. nov. Radular teeth of specimen from South Africa, SAM A35279. A. Dorsal view, scale = 20 μm. B. Lateral view, scale = 15 μm. C. Ventral view, scale = 10 μm.

moved, Adlam's Reef, Sodwana Bay National Park, Natal, South Africa, 1 m depth, 9 May 1982, T. M. Gosliner. CASIZ 078647, one specimen, dissected, Hekili Point, Maui, Hawaiian Islands, 1 m depth, 22 May 1991, C. Pittman.

ETYMOLOGY. — This species is named for the multiple bands of pigment found on and below the parapodial margins.

DISTRIBUTION. — South Africa (Gosliner, 1987), windward and leeward Hawaiian Islands (present study).

EXTERNAL MORPHOLOGY. — The living an-

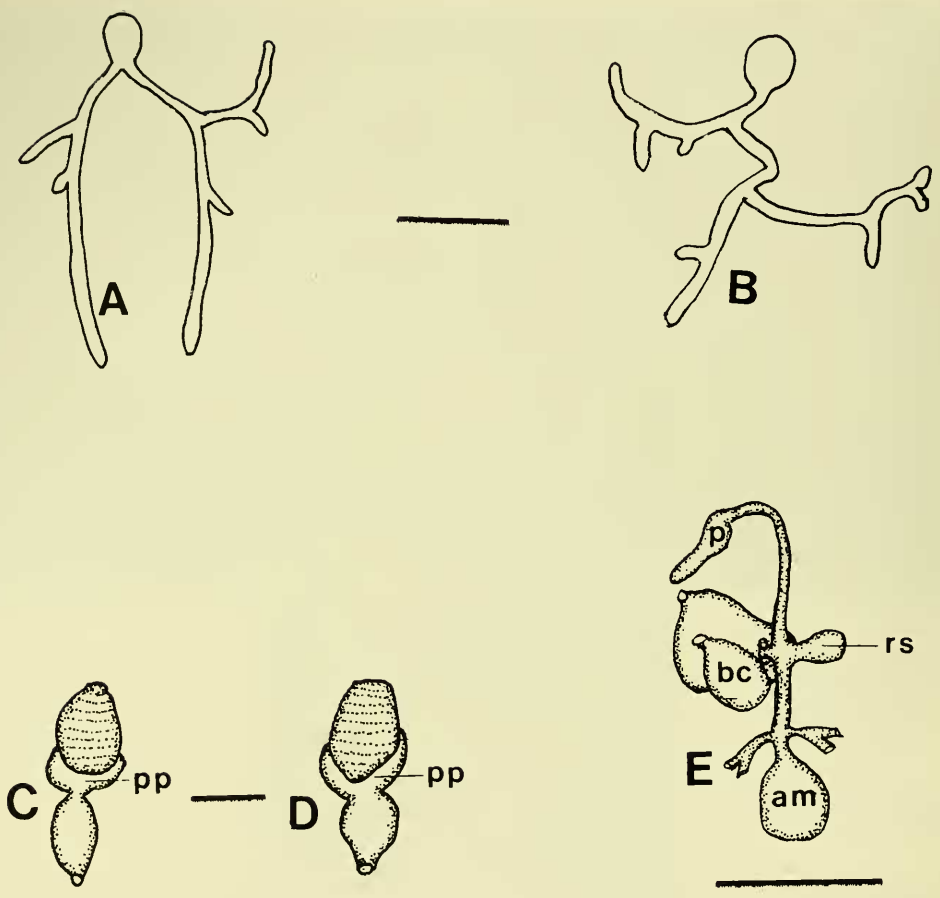

FIGURE 36. *Thuridilla multimarginata* sp. nov. A., B. Branching of pericardial vessels, scale = 5.0 mm. C. Dorsal view of buccal mass. D. Ventral view of buccal mass. C., D. pp = pharyngeal pouch, scale = 0.25 mm. E. Ventral view of distal reproductive organs, am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

imals (Fig. 29E) are light to dark green. The parapodia contain a sequence of several undulating bands or series of interrupted bands. The margin contains interrupted spots of opaque white. Below that, is a series of interrupted patches of bright orange. Ventral to this level, are a series of thin undulating bands of black, reflective blue and black. The head and most of the rhinophores have opaque white pigment with a black tip. The specimen from southern Africa has more diffuse black pigment while the Hawaiian specimens have some green and opaque white on most of the rhinophores with black at the apex. The anterior margin of the foot has orange, black, blue and black lines.

PERICARDIUM AND DORSAL VESSELS. — Lateral vessels are absent (Figure 36A, B). The posterior vessels have a common origin from the pericardium. In the South African specimen, there are 2 undivided or bifurcate vessels emerging from each posterior vessel. In the Hawaiian specimen, the branching pattern is irregular and asymmetrical, with three undivided to trifid branches.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 36C, D) is much smaller than the muscular portion and is barely visible when viewed dorsally. The esophageal pouch

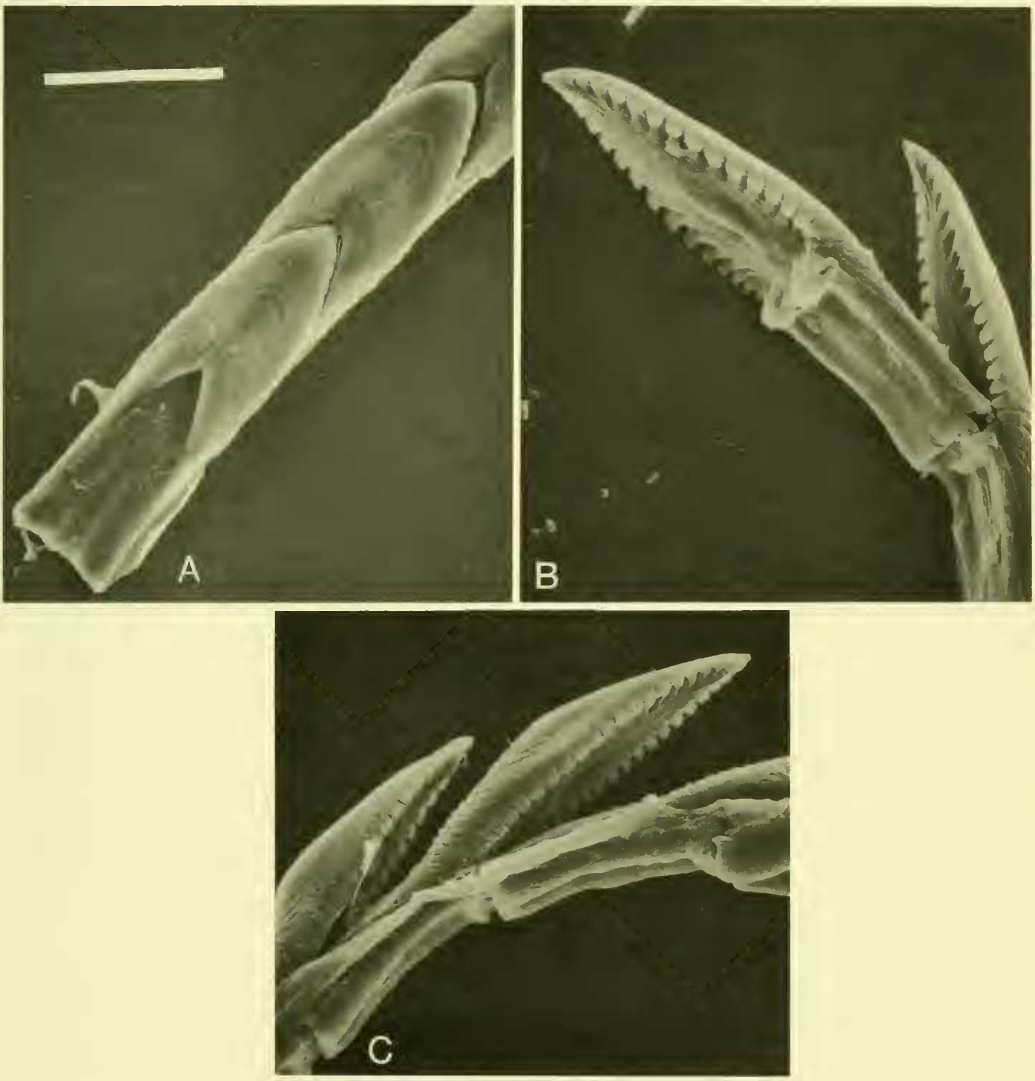

FIGURE 37. *Thuridilla multimarginata* sp. nov. Radular teeth. A. Dorsal view of specimen from South Africa, SAM A35282, scale = 43 μm. B. Lateral view of same specimen, scale = 30 μm. C. Ventral view of specimen from Hawaii, CASIZ 078647, scale = 25 μm.

is ovoid, almost as large as the buccal mass. The radula was examined in one specimen from South Africa and one from Hawaii and consists of 24–29 teeth. Neither specimen had any teeth in the ascus. The ventral limb had 18 and 22 teeth and the dorsal one had 6 or 7 teeth. The teeth (Fig. 37) are 83–103 μm in length. They are broad and triangular with 18–21 coarse denticles along either side of the cutting margin. The denticles continue dorsally as striations. The dorsal surface of the tooth (Fig. 37A) has a prominent triangular cavity where the cutting portion of the adjacent tooth fits snugly. The basal portion of the tooth is slightly shorter than the cutting one. The posterior end of the tooth is largely flat, without a distinct indentation.

REPRODUCTIVE SYSTEM (Fig. 36E). — The ovotestis, prostate and albumen glands are dif-

fuse and are arranged as in *T. bayeri*. Their ducts join the spherical ampulla and the female gland mass. At this point, there is also a junction of the short duct of the spherical receptaculum seminis. The large bursa copulatrix empties via a short duct into a separate gonopore and contained large masses of spermatozoa in both specimens examined. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed penis. The penis is wider proximally and abruptly narrows near the middle of its length.

DISCUSSION. —*Thuridilla multimarginata* retains some of the least derived anatomical features. The buccal mass is highly muscularized with a proportionately small pharyngeal pouch. It has large, wide radular teeth with a prominent dorsal notch. Other aspects of its morphology are highly derived. The lateral pericardial vessels have been lost and the posterior vessels have a common insertion with the pericardium. The radular teeth have striations that extend from the denticles on to the surface of the tooth. The duct of the receptaculum seminis is elongate.

In its external morphology, *T. multimarginata* most closely resembles *T. indopacifica* and *T. livida*. All three species have orange, black and blue parapodial lines. *Thuridilla multimarginata* has additional white pigment and an additional black and orange line that are not present in either other species. In addition, *T. indopacifica* and *T. livida* lack the plesiomorphic features described above for *T. multimarginata*.

DISCUSSION

Phylogeny of the Elysiidae

The systematics and phylogeny of the Indo-Pacific Elysiidae have been recently discussed by Jensen (1992). She critically discussed the morphological variability and polarity of some forty characters within the Elysiidae. Many of these characters are autapomorphic within elysiid taxa or may be resolved within sacoglossan clades below the level of the Elysiidae. Characters which are informative in resolving elysiid phylogeny are listed in Table 1. Their polarities have been discussed by Jensen and will not be repeated here. In some cases, characters have been excluded from consideration since they cannot be adequately polarized using the stiligeroids as an outgroup. For example, Jensen considered a dorsal anus plesiomorphic within the Elysiidae, as the majority of stiligeroid genera have a dorsal anus. However, species of several genera including *Mourgona* and *Caliphylla* have a lateral anus. One cannot resolve the polarity of this character within the Elysiidae using the stiligeroids as an outgroup in the absence of a stiligeroid phylogeny. Presence of a feature in the majority of the outgroup is not sufficient to consider it plesiomorphic. Within the Elysiidae, a dorsal anus is present only in *Placobranchus*. In the resulting phylogeny of the Elysiidae (Fig. 38), it is less parsimonious to consider the dorsal anus plesiomorphic than apomorphic. For the dorsal anus to be considered plesiomorphic requires three steps within the tree, while considering it apomorphic requires a single step.

In addition to the characters considered by Jensen, two others were included in the present analysis. In the branching of the vessels of the pericardium there may be multiple vessels, few vessels or no vessels. In stiligeroids, there are 3 or more vessels emanating from either side of the pericardium. This is considered the plesiomorphic arrangement for the Elysiidae. In elysiids, the radular teeth may have denticles or entirely lack them. When present, the denticles may be small serrations or large rectangular cusps. Rectangular cusps are not found in stiligeroids, though the denticles of some species of *Cyerce* are more broadly triangular. Rectangular cusps are considered apomorphic within the Elysiidae.

Species of *Elysia* are variable for several characters. For this reason, four different species of *Elysia* which depict the range of variation were included in the analysis.

The condition of the parapodia is treated here as the only multistate character. In *Bosellia*, parapodia are absent while in *Elysiella* the parapodia are reduced. In the remainder of taxa, the parapodia are well developed. This character was treated as unordered and no *a priori* judgments were made as to whether the absence of

Table 1. Characters and states for the phylogeny of the Elysiidae

Character	plesiomorphic	apomorphic
1. parapodia	wide	short, absent
2. dorsal lamellae	absent	present
3. foot sole	with margin	indistinct margin
4. pericardium	short	elongate
5. pericardial vessels	3 or more	2 or less
6. ascus muscle	short	long
7. pharynx	large	small
8. pharyngeal pouch	present	absent
9. tooth shape	triangular	blade-shaped
10. denticles	small	large
11. penial stylet	present	absent
12. ampulla	hermaphroditic duct	separate duct

Character #	1	2	3	4	5	6	7	8	9	10	11	12
ancestor	0	0	0	0	0	0	0	0	0	0	0	0
E. papillosa	0	0	0	0	0	1	0	1	1	0	0	1
E. timida	0	0	0	0	1	1	0	1	1	0	1	1
E. ornata	0	0	1	0	0	1	0	1	1	0	1	1
E. trisinuata	0	0	0	1	0	1	0	1	1	0	1	1
Tridachia	0	0	0	0	0	1	0	1	1	0	1	1
Tridachiella	0	0	0	0	0	1	0	1	1	0	1	1
Elysiella	1	0	0	1	0	1	0	1	1	0	1	1
Pattyclaya	0	1	0	1	0	1	0	1	1	0	1	1
Thuridilla	0	0	1	0	1	0	1	0	0	1	1	1
Placobranchus	0	1	1	0	1	0	1	0	0	1	0	1
Bosellia	2	0	0	0	0	0	0	0	0	0	0	0

parapodia in *Bosellia* is plesiomorphic or due to secondary loss.

In her analysis of the Elysiidae, Jensen focused on Indo-Pacific taxa and did not consider the genera *Tridachia* and *Tridachiella* in her detailed discussion of phylogenetic relationships. For the purposes of this discussion, these taxa are considered in addition to the taxa treated by Jensen. Specimens of *Tridachia crispata* Mörch, 1863 (CASIZ 067560, Roatan) and *Tridachiella diomdedea* (Bergh, 1894) (CASIZ 066938, Bahía de los Angeles, Baja California) were examined to compare with the described anatomy of these species.

Jensen (1992) considered *Bosellia* as a member of the same clade as the elysiids. However, she contended that it should not be considered as a member of the Elysiidae, since it lacks parapodia, a separate ampulla or a highly branched prostate, all obvious apomorphic characters of the family. Jensen noted that while lacking parapodia, species of *Bosellia* have a densely branched digestive gland and a ciliated groove that continues across the foot sole and considered these as synapomorphies of *Bosellia* plus the Elysiidae. Whether one considers the Elysiidae to be diagnosed by the possession of densely branched digestive gland or parapodia is entirely arbitrary. However, the fact remains that *Bosellia* is more closely related to other elysiids than to any other sacoglossan. Rather than include the genus *Bosellia* in its own

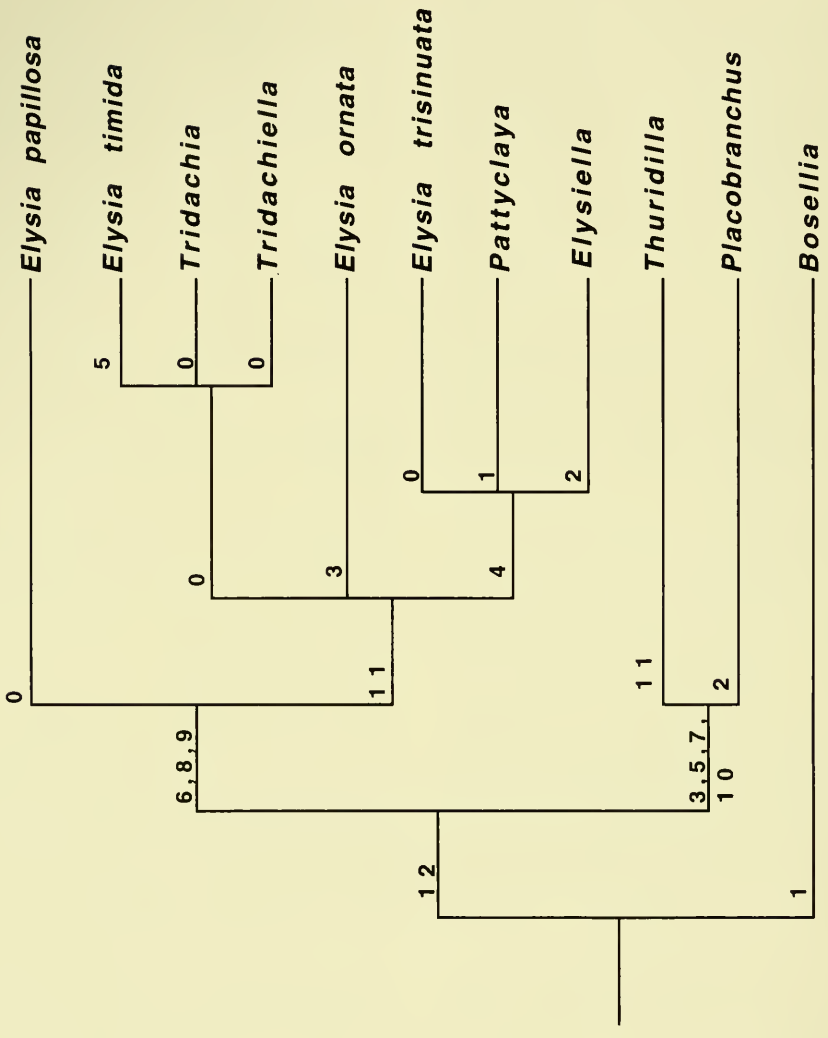

FIGURE 38. Phylogeny of the Elysiidae, numbers refer to characters listed in Table 1.

monogeneric taxon, I prefer to consider all of the descendants of the common ancestor with densely branched digestive gland and ciliated groove expanded to form a foot sole to represent the Elysiidae.

When the characters listed in Table 1 were analyzed using PAUP version 3.1, a single tree was produced (Fig. 38). The thirteen variations of the tree produced using this version of PAUP are all resolved into the single tree depicted here when branches not supported by apomorphies are collapsed. This tree has a consistency index of 0.722. From this tree several things regarding the phylogeny of the Elysiidae are evident. *Bosellia* is the least derived member of the clade, in that the ampulla is plesiomorphic. *Placobranchus* and *Thuridilla* represent a well-supported clade that is clearly

distinct from the other well-supported clade containing *Elysia*, *Elysiella*, *Pattyclaya*, *Tridachia* and *Tridachiella*.

Within the second clade, there is little resolution of phylogeny. However, separation of the genera *Pattyclaya* and *Elysiella* renders *Elysia* paraphyletic since no apomorphic characters are shared by all members of *Elysia*. This fact was first noted by Jensen (1992) and is also the case in the present analysis based largely upon her investigation. *Tridachia* and *Tridachiella* have been separated from *Elysia* on the basis of their undulate parapodia. MacFarland (1924) described *Tridachiella* as distinct from *Tridachia*, as the parapodia were not joined anteriorly. However, all other elysiids with parapodia have them unjoined, and this is clearly plesiomorphic. MacFarland indicated that the anus of *Tridachiella* was situated near the pericardium rather than laterally, but did not discuss the systematic relevance of this apparent difference. Re-examination of *Tridachiella diomedea* here indicates that MacFarland was in error. The anus of *T. diomedea* is lateral, as in all elysiids other than species of *Placobranchus*. Maintenance of *Tridachia* as a distinct genus renders *Tridachiella* paraphyletic, as there are no autapomorphic features which support it. Jensen (1992) noted that these genera are all monotypic except for *Pattyclaya*, which includes two species. Based on the present phylogenetic analysis, *Tridachiella*, *Tridachia*, *Elysiella* and *Pattyclaya* are regarded as synonyms of *Elysia*, as this is the oldest name for the most inclusive monophyletic group. *Elysia* represents a large and morphologically diverse taxon. Further phylogenetic analysis of this taxon is needed to ascertain whether monophyletic subclades do in fact exist.

The monophyletic group containing *Thuridilla* and *Placobranchus* is supported by four apomorphies, a modified foot sole, reduced lateral pericardial vessels, a small pharynx and presence of rectangular denticles on the teeth. The latter two of these are unique to members of this clade, while the first two have also arisen independently within *Elysia*. *Placobranchus* has several synapomorphies shared by members of the taxon including: a broad head, well-developed longitudinal dorsal lamellae, median eyes, dorsal anus, and reduced pericardial vessels. *Placobranchus* has been regarded as a monotypic genus containing only *P. ocellatus* van Hasselt, 1824 and its many synonyms. Another undescribed species has been found in the western Pacific and will be treated in a separate paper.

Species of *Thuridilla* also share several apomorphic features: elongate rhinophores, single, thick, darkly pigmented ampulla, non-muscular, unarmed penis, bursa copulatrix with separate gonopore and orange or red eggs. Bright coloration, indicated as an autapomorphy of *Thuridilla* by Jensen (1992), is not an autapomorphy for the taxon, as some species are more drably colored (see subsequent discussion of *Thuridilla*), thus retaining the plesiomorphic state. The above phylogeny and the autapomorphic features described for *Thuridilla* indicate that it is indeed a monophyletic taxon within the Elysiidae.

Aspects of the ecology of these species are interesting in light of the hypothesis of phylogeny presented here. Virtually all of the least derived sacoglossans are intimately associated with siphonaceous chlorophytes of the genus *Caulerpa*. Several workers (Gosliner, 1987; Clark and DeFreese, 1987) have suggested that the sacoglossans have undergone most of their adaptive radiation on *Caulerpa*. Most species of *Elysia* (including species originally considered as *Tridachia*, *Tridachiella*, *Elysiella* and *Pattyclaya* but here included in *Elysia*) are intimately associated with their algal food and are usually cryptic upon their food. Species are not often observed crawling away from their preferred food. In contrast, species of *Placobranchus* and *Thuridilla* are generally observed crawling freely in the open, and have not been observed in association with particular algae. *Placobranchus* spp. are found crawling partially buried under fine silty sediment while species of *Thuridilla* are found on shallow reefs. It appears that the morphological divergence noted in the proposed phylogeny is mirrored in their ecological radiation. Little is known about the relative palatability of *Elysia*, *Placobranchus* and *Thuridilla*, but species of *Thuridilla* are brightly colored and readily observed in the open, while species of *Elysia* and *Placobranchus* are generally cryptic. This might suggest that species of *Thuridilla* have better developed chemical defense mechanisms

Table 2. Tooth length in *Thuridilla* species

Species	Tooth length (in μm)
bayeri	40-50
lineolata	27-40
livida	40
moebi	43
splendens	40-60
vatae	40-60
virgata	50
carlsoni	105-115
kathe	52-59
flavomaculata	60
hoffae	50
albopustulosa	30
undula	33-47
indopacifica	30-44
multimarginata	83-103
neona	45-50
picta	56
hopei	45-60
decorata	34

and may be employing aposematic warning coloration. This hypothesis certainly requires testing in both field and laboratory situations.

Morphological variability in *Thuridilla* and polarity of characters.

In examining the morphological variability within *Thuridilla*, species of *Placobranchus* and *Elysia* were considered as outgroups for determination of polarity. Twenty-three characters were determined to be informative, though two were autapomorphic and were excluded from cladistic analysis. Data from the literature (primarily from the recent work of Jensen (1992)) was used for *T. hopei* (Verany, 1853) and *T. decorata* (Heller and Thompson, 1983). The remaining species were examined from specimens in the collections of the California Academy of Sciences. In addition to the species described here, a specimen of *T. picta* (Verrill, 1901) was examined, as its anatomy had not been completely described. Anatomical data was available for all known species of *Thuridilla* with the exceptions of *T. caerulea* (Kelaart, 1858), *T. gracilis* (Risbec, 1928) and *T.* sp. 75 of Wells and Bryce (1993). The following characters were considered:

1. Ground color. — Virtually all species of *Elysia* and *Placobranchus* have a uniformly green body color. Several species of *Thuridilla* are greenish while others have brightly colored general body color. This is also true of most other sacoglossans. Here green is considered plesiomorphic while other colors are considered derived.

2. Tooth size. — In virtually all species of *Elysia* and *Placobranchus*, the radular teeth are large, more than 100 μm in length. Within the *Thuridilla*, only *Thuridilla carlsoni* and *T. multimarginata* have teeth of this size. In the remaining species, the teeth are smaller than 75 μm (Table 2). This latter state is considered apomorphic.

3. Buccal mass size. — In all species of *Elysia* a pharyngeal pouch is absent. In *Placobranchus*, the anterior muscular portion of the buccal mass is larger than the pharyngeal pouch. This is also the case in *T. carlsoni*, *T. multimarginata* and *T. kathae* and *T. flavomaculata*. In the remaining species of *Thuridilla*, the muscular portion is equal to or smaller than the pharyngeal pouch. A proportionately larger pharyngeal pouch is considered derived.

4. Dorsal notch. — Most species of *Elysia* have a prominent notch on the dorsal surface of the tooth where the acute end of the adjacent tooth abuts. A notched tooth is present in most stiligeroids as well. The radular teeth of *Placobranchus* lack a deep notch. In *Thuridilla carlsoni* and *T. multimarginata*, a prominent dorsal notch is present. This is considered plesiomorphic in *Thuridilla*. In the remaining species, the notch is reduced or entirely absent and is considered apomorphic.

5. Lateral pericardial vessels. — In many species of stiligeroids and most species of *Elysia* there are three or more pairs of lateral vessels emanating from the pericardium. In some species of *Elysia*, the number of vessels is smaller. In *Elysia timida*, for example, only the posterior pair of vessels is present. In *Placobranchus*, no vessels are present. In species of *Thuridilla*, two pairs of vessels may be present or only the pos-

terior pair remains. A single pair of vessels is considered apomorphic, although the character is variable within *T. livida*.

6. Branching of lateral vessels. — In species of *Thuridilla* the lateral vessels from the pericardium, when present, may be highly branched or poorly ramified. Both conditions occur in species of *Elysia*. As there is a trend towards reduction in the degree of branching of the vessels in stiligeroids and species of *Elysia*, reduction in branching or complete loss of lateral vessels are considered apomorphic for *Thuridilla*.

7. Insertion of posterior vessels. — In most *Elysia* and all stiligeroids, the right and left posterior vessels enter the pericardium separately. This condition also occurs in several species of *Thuridilla*, although it may vary in species such as *T. bayeri* and *T. hopei*. In some species of *Thuridilla*, the vessels join and have a common insertion into the pericardium. This configuration is unique to these species of *Thuridilla* and is considered apomorphic.

8. Posterior end of radular tooth. — All species of *Elysia* and *Placobranchus* have a distinctly indented posterior margin of the tooth. This is also true of species of *Thuridilla*, with the exception of *T. multimarginata*, which has a straight posterior margin. Presence of a straight margin is considered autapomorphic and was not included in the phylogenetic analysis of *Thuridilla*.

9. Articulating lobes on radular teeth. — In species of *Elysia* and *Placobranchus* the posterodorsal portion of the tooth has a simply rounded surface. This is also the case in the radular teeth of *Thuridilla carlsoni* and *T. multimarginata*. In the remaining species of *Thuridilla*, the posterior portion of each tooth is expanded into a pair of rounded articulating lobes with a separtion of the posterodorsal and posteroventral portions of each tooth. This is considered apomorphic for these members of the genus.

10. Number of denticles on radular teeth. — Some species of *Elysia* have numerous minute denticles on the sides of the cutting margin of the teeth, while others have smooth margins. Most members of this genus have a row of small medial denticles. In species of *Placobranchus* and *Thuridilla*, the denticles are wide and rectangular. This character is a synapomorphy for these taxa. In species of *Placobranchus*, there are about 8–15 denticles on either margin of the tooth. In most species of *Thuridilla*, there are about 20 denticles on either side of the cutting margin. In *T. carlsoni* there are 35–38 denticles on either side of the tooth. This is considered autapomorphic for this species and is excluded from the cladistic analysis.

11. Striations on teeth. — In some species of *Thuridilla*, the spaces between the denticles continue as linear depressions that extend onto the lateral and dorsal surface of the teeth, creating striated teeth. Other species of *Thuridilla* lack these striations as do all species of *Elysia* and *Placobranchus*. Therefore, presence of striations on the teeth of some species of *Thuridilla* is considered apomorphic.

12. Extension of denticles on cutting margin of tooth. — In several species of *Elysia*, both *Placobranchus* and most species of *Thuridilla*, the denticles on the tooth extend from the lateral margin of the tooth and continue ventrally as extended denticles. In a few species of *Thuridilla*, such as *T. neona* (Fig. 33B), the distal end of denticles is flush with the lateral margin of the tooth. This is considered apomorphic for these species of *Thuridilla*.

13. Relative size of buccal mass and pharyngeal pouch. — In character 3, a muscular portion of the buccal mass was larger than or equal to the pharyngeal pouch in the plesiomorphic state, while in other derived species the buccal mass was smaller than than the pharyngeal pouch. In this transformation, based on the sizes of the muscular portion of the buccal mass and pharyngeal pouch, it appears that the buccal mass retains its original size and that the pharyngeal pouch becomes slightly larger. In some species of *Thuridilla* the pharyngeal pouch is much larger than the buccal mass. This appears to be due to additional enlargement of the pharyngeal pouch coupled with reduction in the size of the muscular portion. Since this occurs

by both enlargement of the pharyngeal pouch and reduction of the muscular portion of the buccal mass, it is considered as a character transformation distinct from simple enlargement of the pharyngeal pouch. This increase in relative and actual size of the pharyngeal pouch is considered apomorphic.

14. Receptaculum seminis duct. — The organ for storage of sperm in most Elysiidae that connects to the female gland mass has been considered by Sanders-Esser (1984) and Jensen (1992) as a genital receptaculum rather than a receptaculum seminis, since it does not contain oriented spermatozoa. However, its position in most species of *Elysia* and *Placobranchus*, entering the junction of the ampulla the female gland mass and vas deferens, is identical to that of the receptaculum seminis of other sacoglossans and many other opisthobranchs. It appears to be a structure homologous to the receptaculum owing to its similar position, though its function may have been altered. Because of the likely homology, it is referred to as a receptaculum seminis in this study. Jensen (1992) also considered the stalked structure found in *Elysiella pusilla* a genital receptacle. It differs from the other genital receptacle in that it is situated at the distal end of the female gland mass, near the female genital aperture. This is far more likely homologous with the bursa copulatrix of less derived sacoglossans such as *Volvatella*, despite its histological similarity to the more proximal receptical of all other elysiids.

The structure referred to as a bursa copulatrix by Jensen (1992) and here may not be homologous to the bursa copulatrix of other sacoglossans such as *Volvatella*, with a less derived reproductive system and that described above for *Elysiella pusilla*. The bursa of *Thuridilla* differs from that of all other sacoglossans in that it opens via a separate gonopore adjacent to the female gland mass. It also appears to be permanently present in mature individuals while other bursae in other elysiids are transitory and appear only following copulation. These secondary bursae have been found only in species with hypodermic impregnation (Jensen, 1992). Certainly more detailed study of the various genital receptacles found in the Sacoglossa is necessary to more firmly establish homology.

In species of *Thuridilla*, the duct of the receptaculum seminis may be long or short. Species of *Placobranchus* and *Elysia* have elongate receptaculum ducts. An elongate duct in *Thuridilla* is considered plesiomorphic.

15. Cream or yellow parapodial marginal band. — No species of *Elysia* or *Placobranchus* have a cream or yellow band along the margin of the parapodia. In *Thuridilla carlsoni*, *T. kathae* and *T. flavomaculata*, a band that varies from cream to yellow to orange-yellow may be present. This is not found in other species of *Thuridilla* and is considered apomorphic for the genus.

16. Orange, black and blue parapodial marginal bands. — No species of *Elysia* or *Placobranchus* has a combination of these three colored bands, yet they are present in several species of *Thuridilla*. Two species of *Elysia*, *E. ornata* and *E. grandifolia*, have orange and black marginal lines. However, it is apparent from the phylogenetic analysis presented in (Fig. 38) that *E. ornata* is a more derived species of *Elysia*. Presence of the orange, black and blue lines in the same sequence is considered apomorphic for species of *Thuridilla*. Three other species have orange, black and blue pigment on the parapodia. In *T. lineolata*, the blue is a light blue color rather than the "electric" reflective pigment found in other species of *Thuridilla*. In *T. undula* and *T. neona*, the orange is a subdued burnt orange undulating band rather than a straight line composed of reflective granules. Owing to these deferences, these three species are not consdered apomorphic for this character, as this appears to be a non-homologous similarity.

17. White longitudinal parapodial lines. — No species of *Elysia* or *Placobranchus* have a series of white longitudinal lines on the surface of the parapodia. Such lines are present in *T. bayeri* and *T. splendens* and are considered apomorphic.

18. Bluish body color. — All species of *Elysia* and *Placobranchus* have a basically green body color. Several species of *Thuridilla* have a bluish body color. This is considered

apomorphic.

19. White head with orange or red rhinophores. — This feature is only found in a few species of *Thuridilla* and in no other elysiids. Presence of this pigment combination is considered apomorphic.

20. Connections between lateral and posterior vessels. — In some species of *Thuridilla* branches of the lateral pericardial vessels join with branches of the posterior vessels. This condition also occurs in a few species of *Elysia* with an elongate pericardium. As an elongate pericardium is probably a derived feature within the Elysiidae, it is logical to assume that connections between vessels are also apomorphic. Having connections of the lateral and posterior vessels is also considered apomorphic within *Thuridilla.*

21. Orange undulating margin of the parapodia. — No species of *Elysia* or *Placobranchus* have an undulating burnt orange margin to the parapodia. Thus, this condition found in *Thuridilla undula* and *T. neona* is considered apomorphic.

22. Black body color. — *Thuridilla livida* and *T. hoffae* are the only elysiids with a black body color. Presence of this pigment is considered apomorphic for these species.

23. Width of teeth. — The radular teeth of *Placobranchus* are of moderate width. Also the radular teeth of most caliphyllid stiligerids (excluding *Caliphylla*) are wide. Wide teeth occur in *Thuridilla carlsoni*, *T. multimarginata* and *T. neona*. Narrow teeth are found in the remainder of species and are considered apomorphic within *Thuridilla.*

Phylogeny of *Thuridilla*

Based on the polarities discussed above, the distribution of plesiomorphic and apomorphic character states is found in Table 3. These data were analyzed using PAUP version 3.1. A single most parsimonious tree was found (Fig. 39). This tree had a consistency index of 0.477 and a length of 44 steps. A consistency index of 0.477 means that more than half of the characters were subject to at least one instance of homoplasy, either parallelism or reversal. Several apomorphies exhibit no instance of parallelism or reversal. They include: reduction of tooth size, increase in size of the pharyngeal pouch, reduction of the dorsal notch of the radular teeth, presence of articulating lobes on posterior end of radular teeth, denticles flush with cutting edge of tooth, buccal mass reduced in size, presence of opaque white lines on body, head white with orange or red tentacles, lateral vessels connecting with posterior ones and body black. The following characters exhibit parallelism in the apomorphic state: ground color other than green, lateral pericardial vessels lost, posterior vessels with a common insertion into the pericardium, striations present on dorsal surface of tooth, duct of receptaculum seminis short, cream or yellow parapodial margin present, orange, black and blue parapodial margins present, body bluish, orange undulating band present.

Five characters exhibit one instance of reversal to the plesiomorphic state: lateral pericardial vessels many, separate insertion of posterior vessels, length duct of receptaculum long, orange, black, and blue parapodial bands absent and radular teeth wide.

Use of characteristics of color patterns is controversial in phylogenetic reconstruction. For this reason, a separate phylogeny was produced, which excluded all characters that are related to color. The basic topology of the tree is very similar to the tree produced using characteristics of color pattern. The primary difference is that there is poor resolution of taxa within the two large clades that are determined by apomorphies of character 18 and characters 5, 11 and 16. The fact that the tree topology is essentially the same in the absence of color data increases the confidence in adding additional data to enhance resolution, particularly in taxa such as *Thuridilla*, that are not especially character rich.

The pattern of species cladogenesis observed in *Thuridilla*, where there is little adaptive radiation in the lower branches of the tree and more derived clades tend to undergo much more speciation than lower clades, is similar to that found in other opisthobranch lineages. Within the distantly related opisthobranch genera *Flabellina* and *Hallaxa*, the same pattern

Table 3. Character states in *Thuridilla* taxa

character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
bayeri	1	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1
lineolata	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1
livida	1	1	1	1	1	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1
moebii	1	1	1	1	0	1	1	0	1	0	0	0	1	9	0	0	0	1	0	0	0	0	1
splendens	1	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1
vatae	1	1	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1
virgata	1	1	1	1	0	1	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1
carlsoni	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
kathe	0	1	0	1	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1
flavomaculata	0	1	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1
hoffae	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	1	1
albopustulosa	1	1	1	1	0	1	1	0	1	0	0	0	1	1	0	0	0	1	1	1	0	0	1
undula	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1
indopacifica	0	1	1	1	1	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1
multimarginata	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0
neona	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0	1	0	0
picta	0	1	1	1	1	1	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	1
hopei	1	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
decorata	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1

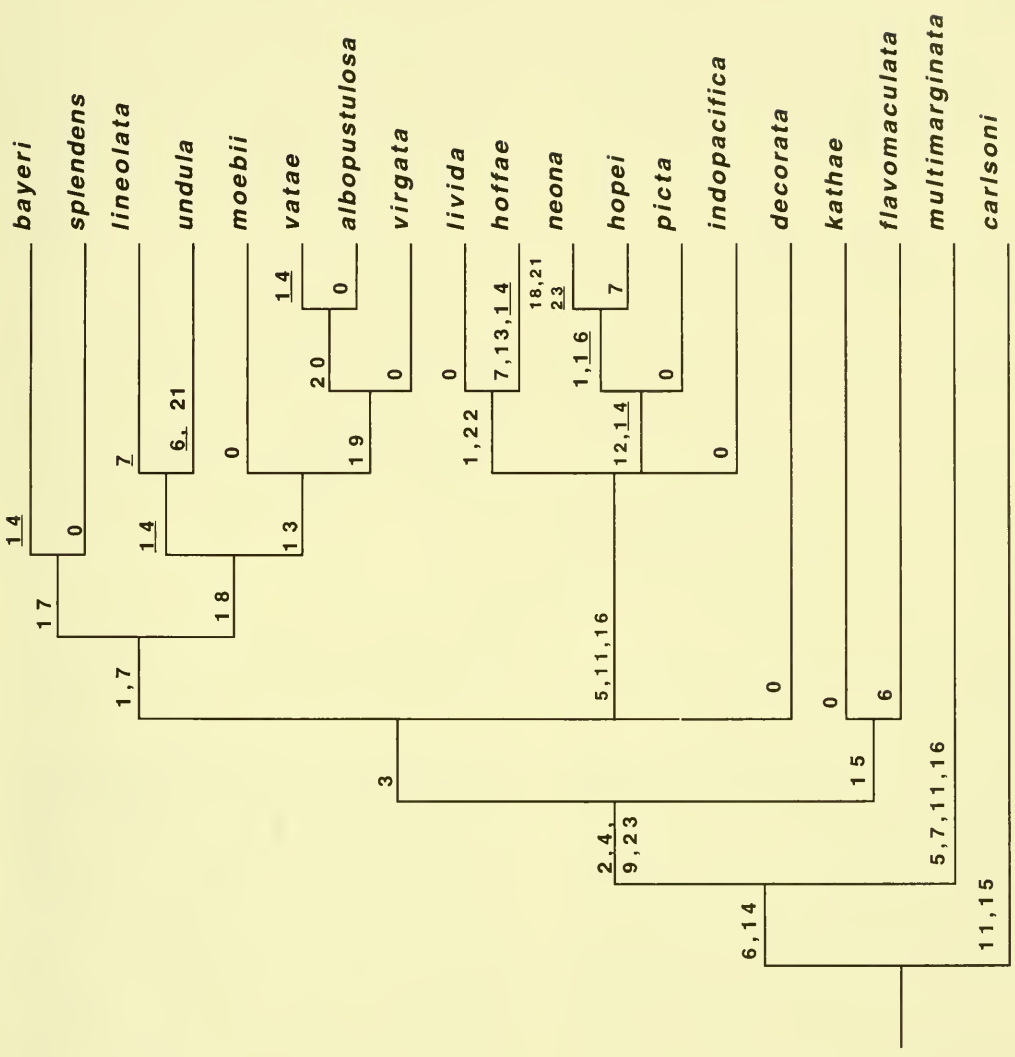

FIGURE 39. Phylogeny of *Thuridilla*, numbers refer to characters discussed in text and present in Table 3. Underlined numbers refer to characters that have undergone reversal.

of speciation tends to occur (Gosliner and Willan, 1991; Gosliner and Johnson, 1994). In *Flabellina*, most of the less derived taxa are polar or temperate, while the clades that have undergone a great deal of adaptive radiation are strictly tropical. This pattern is not as obvious in *Hallaxa*, where some of the less derived taxa are tropical. *Thuridilla*, in contrast is exclusively tropical. Most of the least derived sacoglossans are tropical and some members of more derived clades are present in temperate habitats.

Biogeographical relationships

Previous studies on the phylogenetics of Indo-Pacific opisthobranchs (Gosliner, 1989; Gosliner and Willan, 1991; Gosliner and John-

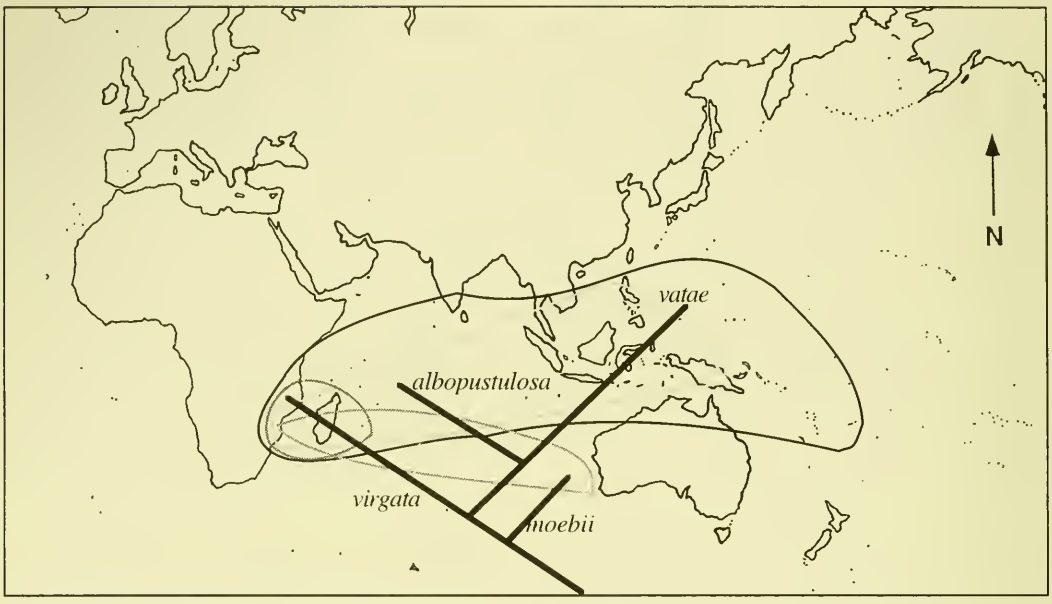

FIGURE 40. Area cladogram of four species of *Thuridilla*.

son, 1994) have demonstrated that sister taxa exhibit little or no vicariance in their present distributions.

When sister species of *Thuridilla* are compared geographically, two clear cut cases of vicariance are apparent. *Thuridilla hopei* from the Mediterranean has an Indo-Pacific sister species (*T. neona*), while *T. picta* from both the eastern and western Atlantic is the sister taxon of *T. hopei* plus *T. neona*. Springer (1982) demonstrated that in Indo-Pacific reef fishes sister species had marked areas of vicariance related to plate boundaries. For example, a species found in the Indian Ocean to the western margin of the Pacific Plate would likely have its sister species restricted to the non-marginal portions of the Pacific Plate. In no instance does that occur within *Thuridilla*. The only species restricted to the non-marginal portions of the Pacific Plate is *T. neona* whose sister species is Mediterranean. Three additional species are apparently somewhat restricted in their distributions. *Thuridilla decorata* is known only from the Red Sea. *Thuridilla lineolata* is known only from Indonesia. The distribution of *T. virgata* is thus far known only from the south western Indian Ocean. Two of these, *T. decorata* and *T. virgata*, have no clear-cut sister species, but are rather the sister taxa to a larger clade. In the case of *T. decorata*, it is the sister taxon to the clade that includes 14 species of *Thuridilla*. *Thuridilla lineolata* is the sister taxon to *T. undula* which has been found from the Maldives, Papua New Guinea, Palau, the Philippines and Guam. *Thuridilla virgata* is the sister species to a clade containing two other species, *T. vatae* and *T. albopustulosa*. All three of these species completely overlap in their distributions in the western Indian Ocean (Figure 40), although the latter two species are more widely distributed to the east. In the remaining cases where sister species are well defined, the species are presently overlapping for most of their ranges. *Thuridilla bayeri* is found from the western Indian Ocean to the Marshall Islands in the central Pacific, while its sister species, *T. splendens* is found only in the western Pacific. The ranges of *T. vatae* and *T. albopustulosa* are shown in Fig. 40, and are almost completely overlapping, except that *T.*

vatae has been found in the Marshall Islands while *T. albopustulosa* has not been found east of the western Pacific margin. *Thuridilla livida* has been found from the western Indian Ocean to the Marshall Islands while its sister species, *T. hoffae* is known from the western Pacific to the Marshalls. *Thuridilla kathae* is known from the western Indian Ocean to the western Pacific, while its sister species, *T. flavomaculata* has been found from the western Pacific to the Marshalls.

Clearly no consistent pattern emerges from these examples. Present distributions have probably expanded from original vicariant ones and this subsequent dispersal masks any early separation of founder populations. Though many of the ranges of these species are probably incomplete, subsequent additional records can only serve to increase the area of overlap for sister taxa.

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